AN INTRODUCTION TO THE STUDY OF THE NERVOUS SYSTEM

THIRD EDITION.

Compendium of Regional Diagnosis in Affections of the Brain and Spinal Cord.

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AN INTRODUCTION TO THE STUDY OF THE NERVOUS SYSTEM

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FOREWORD

For a proper understanding of the functions of the human body it is necessary to have a clear knowledge of its structure. In no system of the body is this more essential than in the Central Nervous System, with its extraordinary powers of interaction and integration, based upon an intricate series of relations and connections. Yet for the ordinary student, graduate or undergraduate, this knowledge is very hardly gained. Contributions to this subject have been made by anatomists, physiologists, histologists and neurologists, and published in their respective books and journals. Much valuable information has remained hidden in these publications on the one hand, whilst on the other statements accepted at one time, but later shown to be incorrect, have been copied from book to book.

During a long experience of teaching it has been proved that it has been extremely difficult for students to try to deal with the multiplicity of authorities and to weigh the value of the contradictory statements in order to obtain the necessary information, and until recently there have been no books containing accepted views to which the student can be referred.

In this volume the text and the diagrams are the outcome of teaching, clinical and laboratory experience, and it gives admirably the much-needed information, and gives it, too, in a form which has already been appreciated by students, and will not fail to appeal to other workers who have but little time. The aspects of the subject adequately presented in ordinary text-books have been more briefly dealt with, whilst others not necessarily of greater importance in themselves have been treated more fully because they involve parts of the subject in which, in the available text-books, there are many gaps between the gross and minute structure and the physiology.

This book should be very helpful to undergraduates working for examinations such as the Second Medical, the Primary Fellowship, and those leading to a final science degree, but it should prove of even greater use to graduate students working for higher examinations, such as the Membership of the Royal College of Physicians, or to those engaged in general clinical practice.

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PREFACE

THIS book, as its title indicates, has been written primarily for students. It is intended to stress particularly the points which we, as teachers, find are not sufficiently clearly expressed elsewhere. In a book intended for such readers no apology therefore is necessary for a certain amount of dogmatism. Brevity and clearness have been our objects. For these reasons controversial matter has been largely omitted, except where it has seemed to us that there is a real difference of opinion. When this occurs we have, as far as possible, stated the opposing points of view.

Minute structure and function have been considered together, but no description of gross structure has been given, as this can be found so admirably expressed in the many modern text-books. Some emphasis has been laid on clinical application, for the sake of hospital students, but neurology and pathology (as such) have been purposely omitted. In order to facilitate references to other books, alternative names have been given where such are in common use, as this book is meant only as an introduction to the study of the Nervous System.

Our thanks are due primarily to Professor Winifred Cullis, who has kindly written the Foreword and given us every encouragement throughout. For the account of recent work on the olfactory nerve connections we are indebted to Professor Elliot Smith and Dr. Una Fielding, and we are deeply grateful to Dr. Linnell, to Dr. Kathleen Sykes and to Mrs. McLellan for their valuable help in criticism and compiling of the Index.

Where other authors have been drawn upon acknowledgment as far as possible has been made in the text.

Finally, we greatly appreciate the helpful consideration given us throughout by our publishers.

E. E. H.
G. M. S.

INTRODUCTION TO AMERICAN EDITION

Teachers of clinical neurology have generally felt the need of giving an introductory course in which the fundamental principles of the anatomy and physiology of the nervous system are reviewed. As a result, the student has the opportunity to erect for himself a foundation on which to strengthen the contact between structure and function and their perversions, the symptomatic expression of which is "clinical neurology."

The facts of the anatomy of the nervous system, learned in the first year, and the nervous system in action, learned as physiology in the second year, are largely forgotten when the first contact with clinical neurology, usually in the third year, takes place. The student is ordinarily advised to review anatomy and physiology or read the introductory chapters in the usual textbooks. The majority of students do neither, because the instruction of the first two years in the nervous system is usually too remote from their present interest; the introductory chapters in the textbooks are too diffuse and the diagrams too complicated, attempting to cover entirely too much ground.

A small, compact, authoritative outline meets the needs of the student admirably—something he can carry about with him for reference, the diagrams of which are interesting, clearly designed to illustrate a few simple but important points. These demands are met in the short textbook entitled "An Introduction to the Study of the Nervous System" by E. E. Hewer and G. M. Sandes. I know of no more informative book within the limits set forth by the authors. The diagrams are clear and interesting, and each one is evidently designed to make clear anatomic facts. For example, the internal capsule is shown by a clear-cut diagram with the sensory and motor fibers in their proper relation to the cortex, midbrain, and corticocerebellar pontine pathway. Nothing further is added and these pathways are clear cut and informative—emphasized in exactly the way that a typical clinical case would cause them to stand out. These tracts, so difficult of orientation as a rule, are made clear and easily understandable. Many other diagrams have the same elements of directness, simplicity, and clinical significance. The text itself is clearly written and direct, avoiding discussion and authoritative quotations.

The clinical contributions of Henry Head on aphasia and sensation are given as reliable guides to the understanding of the clinical pictures which are shown when speech becomes symptomatic of a lesion of the brain and when the sensory pathway is interrupted by disease. The importance of regarding speech as a mechanism of the whole brain rather than as a matter of sharply limited pigeonholing is emphasized without the needless discussion usually found in textbooks.

The many excellencies of this textbook need no further elaboration. With this book as an aid, with the contents remembered, and with its clinical implications digested, the third year student should discover that clinical neurology is a pleasant, interesting, and fascinating part of medicine. Of the many methods to achieve this end which the teachers of neurology have had in mind, none seem so purposive and logical as a reasonably firm foundation of anatomic facts and physiologic principles. This the admirable textbook of Hewer and Sandes provides. With this book in the student's hand, the teacher of clinical neurology should find teaching more interesting and less fatiguing, and the student should find learning equally so.

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PART I

AN INTRODUCTION TO THE STUDY OF THE NERVOUS SYSTEM

CHAPTER I

NERVE CELLS AND NERVE FIBRES

THE structure of the nervous system is complex, and in order to understand its functions it is of importance to grasp both the minute and gross anatomy of its various parts. It appears logical to consider first of all the elements of which the whole nervous tissue is built up, namely, cells and fibres.

A. **Nerve Cells.**

The various types of nerve cells are usually distinguished according to their form, being subdivided into unipolar, bipolar, and multipolar (see Diagram 1).

(*a*) *Unipolar Nerve Cells.*

This type is found chiefly during embryonic development, most neuroblasts assuming this form at some stage of their growth. In the human adult these cells

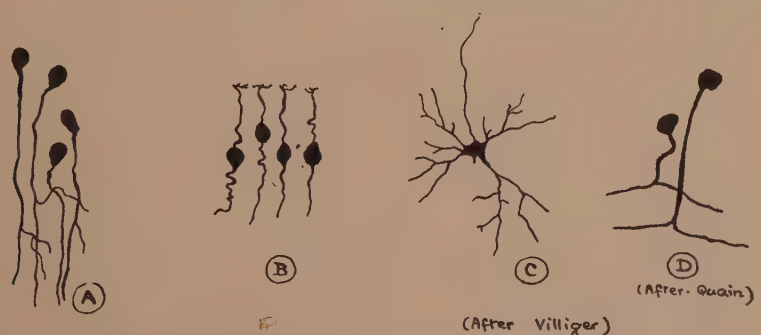

DIAGRAM 1.—Nerve cells of different types.

A. Unipolar cells.
B. Bipolar cells.
C. Multipolar cell.
D. Posterior root ganglion cells.

are only sparsely distributed, being found in the retina and in the mesencephalic nucleus of the fifth cranial nerve.

The cell body is more or less spherical, but with a prolongation at one pole that continues into the single process of the cell.

(*b*) *Bipolar Nerve Cells.*

The typical bipolar cell, with a spherical cell body prolonged at opposite poles into a process, is somewhat rare, being found only in the peripheral nervous system in certain ganglia, such as Scarpa's ganglion and the spiral ganglion of the cochlea, and in the retina.

In mammals the bipolar cells of the posterior root ganglia and of the ganglia on the course of many of the cranial sensory nerves (*e.g.*, Gasserian ganglion) acquire a unipolar appearance, the single process having a T-shaped branching close to the cell ; this is due to the growing round of one process to approximate to and fuse with the other process for a short distance.

(*c*) *Multipolar Nerve Cells.*

This type of nerve cell is the most common and the most important, nearly all cells of the central nervous system being of this form.

The shape of the cell body varies greatly, but in every case there are numerous processes ; one of these processes is usually long and unbranched until its termination, although it may give off collaterals at right angles to its axis, and is known as the axon : the other processes are usually shorter and branch frequently in all planes ; these are known as the dendrites.

The nucleus of the nerve cell is relatively large, and contains at least one nucleolus and not much chromatin. The cytoplasm is granular, the granules being large, strongly basophil, and arranged concentrically round the nucleus and passing into the dendrites ; these are known as Nissl granules. The part of the cell giving rise to the axon is clear of these granules, but frequently contains yellow pigment (especially in the sympathetic ganglion cells and in old age) ; this region is known as the " axon hillock." The whole cell is pervaded by exceedingly fine neurofibrils.

B. **Nerve Fibres.**

The processes of the nerve cells are known as nerve fibres ; in the peripheral nervous system the fibres run together in definite bundles known as nerves. The nerve fibres are usually classified, according to their structure, into medullated and non-medullated fibres (see Diagram 2).

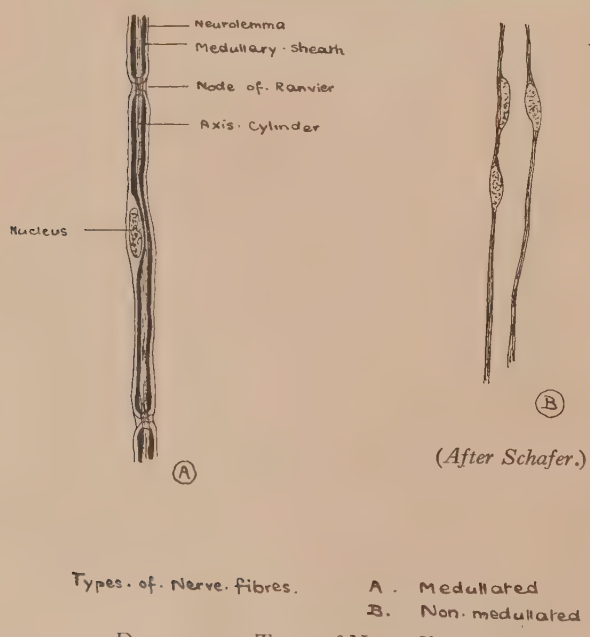

DIAGRAM 2.—Types of Nerve fibres.

(*a*) *Medullated Nerve Fibres.*

The medullated or white fibres consist of a central core —the axis cylinder—which is a direct prolongation of the substance of the cell that gives rise to the fibre. The axis cylinder is enclosed in a fatty sheath (the medullary or myelin sheath) ; this sheath gives the fibre its white appearance, and is interrupted at

regular intervals, producing the nodes of Ranvier. Surrounding the myelin sheath is a thin, nucleated, continuous sheath, known as the neurolemma (primitive sheath or sheath of Schwann); this covering is continuous with the nucleated capsule that encloses each nerve cell in the spinal, cranial and sympathetic ganglia; it is, however, absent from all nerve fibres actually within the central nervous system, a fact of great importance in connection with the recovery of nerve fibres after injury (see Chapter II.). The neurolemmal sheath possesses one nucleus to every internode.

Medullated nerve fibres vary greatly in size, but have all the same structure, whether axons or dendrites, this latter distinction being fundamentally one of function rather than of structure.

(*b*) *Non-medullated Nerve Fibres.*

The non-medullated or grey fibres consist of a central core—the axis cylinder—a prolongation of the cell of origin of the fibre. There is no myelin sheath, but the axis cylinder is directly enclosed in the neurolemmal sheath; in these fibres the nuclei of this sheath appear to be much more numerous than in the case of the white fibres.

THE NEURONE THEORY

The nervous system consists not merely of cells and fibres, but is built up of definite units known as "neurones." A neurone is a nerve cell with all its processes, and this conception of the structure of nervous tissue emphasises the fact that a nerve fibre is merely a part of a nerve cell and cannot function or even exist if separated from its cell.

The actual formulation of this theory is due to Waldeyer (1891), but it is based upon previous researches of His, and of Cajal and Golgi. The former showed that embryologically each neurone develops from one neuroblast cell, the processes being outgrowths from the cell and developing into the nerve fibres. To Cajal and Golgi is due the elaboration of the newer histological methods, including the silver chromate technique, whereby it has become possible to investigate accurately the minute structure and distribution of nerve cells and fibres. By this means it has been shown that degenerative changes following injury are confined to the neurone involved, with no spreading to adjacent cells or fibres. Thus the nervous unit, or neurone, is to be regarded as anatomically and physiologically a single nerve cell.

Connection is established between neurones by contiguity, and not by continuity, and it is important to distinguish between the types of cell process. The dendrites are those processes conveying the nervous impulse *into* the cell from which they are derived, the axon being the process carrying the nervous impulse *away from* the cell. Thus the linkage of neurones is brought about by the mingling of the terminal arborisation of one axon with the dendrites of the next neurone (see Diagram 3). The surface of separation between two neurones is known as the *synapse* (Sherrington), and it is the variations of physico-chemical conditions

at the synapse that explain the characteristics of the reflex arc (see Part II., Chapter VIII.).

A point of extreme importance in understanding the physiological working of the nervous system is that conduction of nervous impulses through a neurone

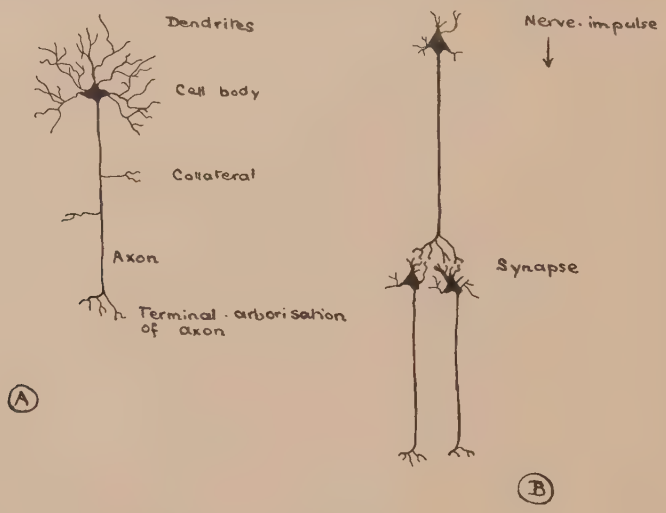

DIAGRAM 3.

A. Schematic representation of a neurone.
B. Schematic representation of junction between neurones.

is always in one direction only, namely, into the cell by the dendrites and away from it by the axon. The nerve impulse cannot pass across a synapse in the reverse direction. This is known as the " law of forward conduction," and follows as a necessary corollary to the physiological conception of the axon and the dendrites.

REFERENCE

SHERRINGTON. " The Integrative Action of the Nervous System," 1906.

For further details of structure, of cell types, and of nerve endings, reference should be made to Quain's " Anatomy " (Schafer), Vol. II., Part I.

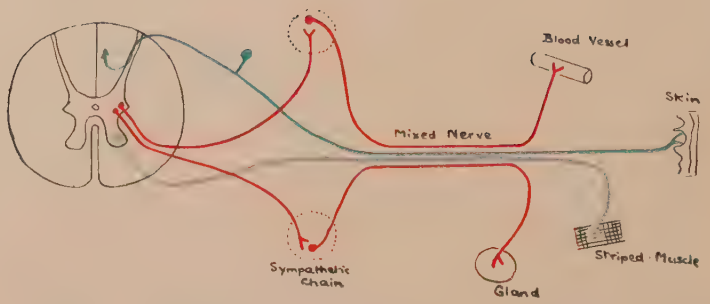

DIAGRAM 4.—Diagram representing the more important Fibres present in a Mixed Nerve.

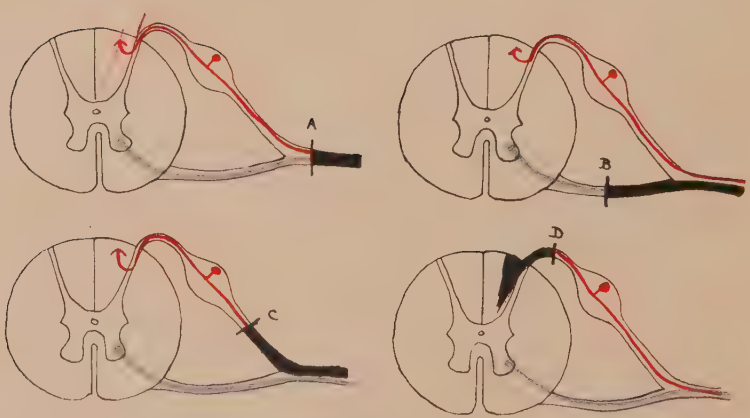

DIAGRAM 5.—Degenerative effects following section of Nerve Roots in various positions. The letter shows the position of the section.

CHAPTER II

CHANGES FOLLOWING SECTION OF NERVES

SECTION of a nerve will produce results varying according to the type of the fibres cut. A mixed nerve usually contains the following fibres :—

(*a*) Motor, arising from anterior horn cells of the spinal cord.

(*b*) Sensory, consisting of long dendrites coming from a sensory surface to their cell in the posterior root ganglion.

(*c*) Pre-ganglionic (white) fibres belonging to the autonomic system, arising from lateral horn cells of the spinal cord.

(*d*) Post-ganglionic (grey) fibres of the autonomic system, arising from one of the sympathetic ganglia.

Thus the mixed nerve carries motor, sensory, secretomotor, vasomotor, trophic and possibly other special nerve fibres (see Diagram 4).

Section of a nerve fibre is invariably followed by degeneration of that portion which is cut off from its cell. This is well seen in the fibres of the spinal nerve roots (see Diagram 5). Section of the nerve distal to the fusion of the roots (*i.e.*, at A) is followed by degeneration of the nerve, all the motor and sensory fibres being cut off from their cells of origin. Section of the anterior root (*i.e.*, at B) is followed by degeneration of the motor fibres of the nerve only. Section of the posterior root distal to the ganglion (*i.e.*, at C) produces degeneration of the sensory fibres of the nerve only, while section of the posterior root between the ganglion and the cord (*i.e.*, at D) is followed by degeneration of the entering posterior root fibres involving their upward passage in the posterior columns of the cord.

A. Degenerative Changes.

The degenerative changes that take place may conveniently be considered as those occurring in the nerve trunk, both peripheral and central to the lesion, in the nerve cells belonging to the fibres involved, and in the organs supplied by the nerve fibres.

1. DEGENERATIVE CHANGES IN THE NERVE TRUNK (see Diagram 6).

(*a*) *Peripheral Part.*

Within twenty-four hours of the injury marked changes begin in the fibres cut off from their cells. Simultaneously the myelin sheath fragments, the axis cylinder breaks up into small portions, and the neurolemmal nuclei increase in number. Very shortly the protoplasm round these nuclei becomes more definite, and the sheath breaks up into numerous separate cells. Some of these neurolemmal cells then become phagocytic, engulf the droplets of myelin and fragments of

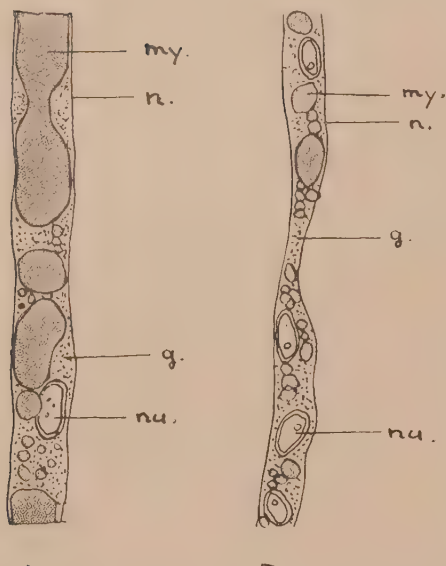

DIAGRAM 6.—Degeneration of Nerve Fibres.

A. Section 50 hours previously.
B. Section 4 days previously.
my. Medullary sheath breaking up into drops of myelin.
n. Neurolemmal sheath.
g. Granular protoplasm replacing myelin.
nu. Nuclei multiplying by division.
Axis cylinder is not shown.
(*After Ranvier.*)

axis cylinder, and pass, full of fat, into the lymph stream. The remainder of the neurolemmal cells then arrange themselves in a row down the middle of the empty sheath, becoming known as the " band fibre," which structure is essential for regeneration of the nerve fibres (see below).

Chemical changes occur in the myelin at the same time as these alterations in appearance. The myelin gives rise to lecithin and kephalin, the latter breaking down into glycerophosphoric acid, choline, and some very unsaturated fatty acids; on the presence of these latter depends the Marchi staining reaction (see Appendix). At the same time the phosphorus content of the tissue diminishes.

(*b*) *Central Part.*

Similar degenerative changes occur also in the fibres central to the lesion, the breakdown spreading up to the next node. At this node the end of the axis cylinder frequently swells, the neurolemma bulging round it. A swelling of this kind may give rise to a neuroma.

2. DEGENERATIVE CHANGES IN THE NERVE CELLS (see Diagram 7).

The nerve cells whose fibres have been cut show degenerative changes which are most marked when the lesion is near the cells of origin. The cell becomes globular, and the nucleus takes up an excentric position. At the same time the Nissl granules disorganise and the staining becomes diffuse (chromatolysis). Later the cell becomes shrunken in appearance, and if no regeneration of the fibres occurs the cell ultimately disappears.

3. CHANGES IN THE ORGANS SUPPLIED.

(*a*) *Muscle.*

The muscles supplied are paralysed, and lose their tone. The muscle substance wastes rapidly, much more quickly than is the case in disuse atrophy. If no regeneration of the nerve fibres occurs, the muscle is ultimately replaced largely by fibrous tissue. The response of the muscle to direct electrical stimulation is altered. A muscle with its nerve supply intact responds to faradic or to galvanic stimulation by a sharp contraction and relaxation, the response at

" make " of the constant current being greater at the kathode than at the anode—*i.e.*, KCC > ACC. When the nerve supply is destroyed the muscle no longer responds to faradic stimulation, but for two to three months it reacts to galvanic stimulation with a slow, slug-like contraction, the response at the anode being now greater than that at the kathode—*i.e.*, ACC > KCC. This alteration of response is known as the " reaction of degeneration," or RD, and is present for several months after the nerve injury.

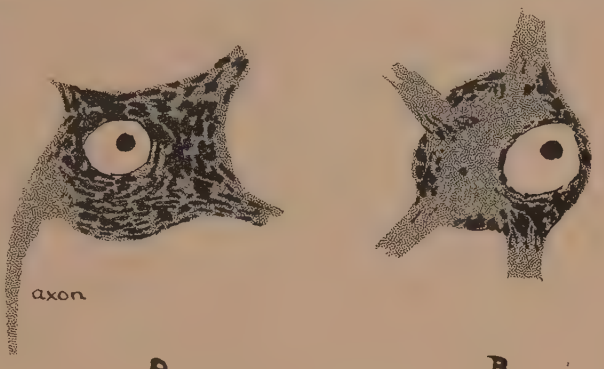

DIAGRAM 7.—Nerve Cells.
A. Normal. B. Showing Nissl Degeneration.
(*After Schafer.*)

(*b*) *Skin.*

There is complete anæsthesia of the part supplied by the nerve, due to interference with the sensory fibres. The skin becomes smooth and shiny, the nails tend to atrophy, and any injury is followed by very slow healing. These changes are in reality trophic, and are due to malnutrition following on disturbance of the vascular supply (see below).

(*c*) *Blood Vessels.*

There is loss of vasomotor control of the blood vessels supplied by these nerve fibres, and consequently loss of tone in the arterioles, and persistent vasodilatation. This leads to a relative stasis, and hence to nutritional changes in the parts supplied, such as the skin.

(*d*) *Glands.*

If the nerve cut contains secretomotor fibres, there is interference with the secretory activity of the gland, which may lead to atrophy of the secreting cells.

(*e*) *Bones.*

If the nerve cut contains fibres supplying bone, the bone substance tends to become rarefied. In the case of a child the growth of the bone is delayed, and the osseous tissue is unusually fragile.

B. **Regenerative Changes.**

Regeneration of nerve fibres is impossible after the death of the cells of origin of the fibres cut. It is also impossible within the central nervous system, due to the absence of neurolemmal covering to the fibres, this structure being essential for regeneration.

Regeneration occurs by downgrowth of the axis cylinder from the central end. The degenerative changes spread back from the lesion on the central side as far as the next node, the fibre thus terminating in a somewhat swollen axis

cylinder covered with neurolemma. This swollen end then puts out pseudopodial-like processes in the direction of the " band fibre." This structure has been shown to exert a chemiotactic influence on the growing axis cylinder, and one of the processes grows down among the neurolemmal cells of the band fibre, ultimately linking up with the original specialised end organ (*e.g.*, myoneural substance, tactile corpuscle, etc.). The neurolemma thus acts as a guide for the growing axis cylinder, at the same time restraining its progress to the correct path. The myelin sheath of the new fibre is acquired later, and the neurolemmal covering is probably formed by growth from the original neurolemmal cells enclosing the uninjured part of the fibre.

The way in which regeneration takes place explains why recovery of function is so extraordinarily complete, as this depends on the re-establishment of connection between the nerve cell and the end organ. It also explains why suture of the cut ends of a nerve soon after injury will assist in regeneration of the fibres, the growing ends of the axis cylinders being thus in immediate contact with the " band fibres." There is never any joining of cut fibres, regeneration being always by downgrowth from the central end. Clearly, regeneration is most likely to be complete if the cut fibres are joined at once ; also, the more remote from the cell that the lesion occurs the better will be the chance of complete recovery.

If the growing end of the axis cylinder is prevented by scar tissue from establishing connection with the band fibre, then regeneration is arrested. If the scar tissue is removed and the two freshened stumps sutured together, regeneration then occurs. This has been known to occur as long as two years after the injury.

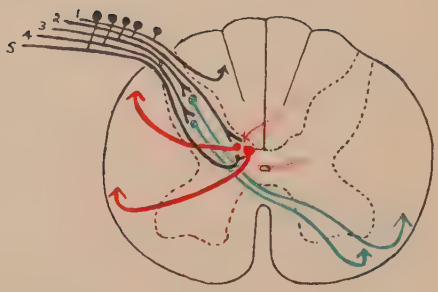

DIAGRAM 8.—Termination within Spinal Cord of Fibres entering by Posterior Root.

1. Passes up by posterior columns to nucleus gracilis or nucleus cuneatus.
2. Ends in Clarke's cells } Relay by direct and indirect cerebellar tracts to cerebellar
5. Ends in Clarke's cells } cortex of same side.
3. Ends in posterior horn cells } Relay by spinothalamic and spinotectal tracts of
4. Ends in posterior horn cells } opposite side to thalamus or to corpora quadrigemina and thence to cerebral cortex.

(*After Herrick.*)

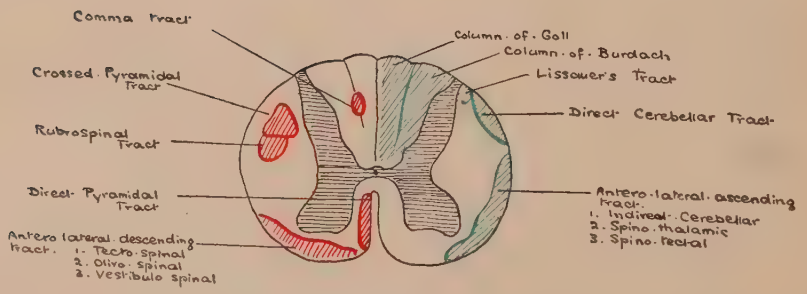

DIAGRAM 9.—Diagram of Cross-Section of Spinal Cord, showing position of Fibre Tracts.

Right : Ascending fibres.
Left : Descending fibres.

CHAPTER III

THE SPINAL CORD: ASCENDING TRACTS

THE fibres ascending in the spinal cord carry impulses from the periphery. There is only one path of entry into the cord, namely, by the posterior root fibres that enter at the posterior horn; some of these fibres run upwards in the cord, such tracts being part of the first neurone on the particular path; other fibres make a cell station in the cord immediately, and for these paths the tract in the cord is the second neurone (see Diagram 8).

Sensory fibres on entering the central nervous system branch into at least two branches, usually an ascending and a descending one. In the cord the descending branch is generally short.

In the following description the tracts are traced up to the cortex of either cerebellum or cerebrum; the interconnections and reflex paths are considered later. (See Diagrams 9 and 10.)

1. COLUMNS OF GOLL AND OF BURDACH (also known as posterior columns).

Fibres enter by the posterior roots, and at once turn upwards, passing in the posterior columns to the lower part of the medulla, where they end. The tract of Goll is derived from the nerve roots of the lower half of the trunk and lower limbs. As they pass upwards they become displaced nearer to the middle line by the fibres from the upper half of the trunk and upper limbs that constitute the tract of Burdach. The fibres of the tract of Goll terminate in the nucleus gracilis, and those of the tract of Burdach in the nucleus cuneatus; these nuclei appear as outgrowths of the central grey matter into the fibre columns, just below the level of the lower border of the olives.

The second neurone arises from the cells of the nuclei gracilis and cuneatus, the fibres crossing at once anteriorly to the central canal as the sensory decussation (or internal arcuate fibres); the crossed fibres take up a position between the olives, and pass upwards as the medial fillet to end in the optic thalamus, gradually becoming more posterior in position as they ascend.

The third neurone arises in the thalamus, passes out by the anterior limb of the internal capsule, and proceeds as part of the corona radiata to end in the post-Rolandic cortex of the cerebrum.

This path from periphery to cerebral cortex thus consists of three neurones, and is a crossed connection.

There is a further connection with the cerebellum. Some fibres arising in the nuclei gracilis and cuneatus pass as external arcuate fibres (some crossed, but mostly uncrossed) to the cortex of the cerebellum by the inferior peduncles.

2. Lissauer's Bundle (also known as marginal bundle).

Incoming posterior root fibres give off a small branch which runs upwards in a position just anterior to the tip of the posterior horns. These fibres run up for a few segments, and then turn into the central grey matter, and end by arborising round cells in this position.

These fibres are connector, and do not carry impulses to higher centres.

3. Direct Cerebellar Tract (also known as dorso-spino-cerebellar, or tract of Flechsig).

This tract lies on the lateral surface of the cord. Entering fibres pass to Clarke's column of cells of the same side at the root of the posterior horn ; here they end. The second neurone arises from these cells, the fibres passing out to the lateral position, where they run upwards, entering the cerebellum of the same side by the inferior peduncle and ending by arborisation in the cerebellar cortex.

4. Gowers' Tract (also known as antero-lateral ascending).

The ascending fibres running in the antero-lateral region of the cord are known collectively as Gowers' tract. This tract comprises three groups of fibres—the spinothalamic, the spinotectal and the indirect cerebellar.

(*a*) *Spinothalamic Fibres.*

Fibres entering by the posterior roots pass in to arborise round cells in the posterior horns, and also in Clarke's column of cells of the same side. The axons of these cells, making the second neurone on the path, cross in the posterior commissure, and run up in the antero-lateral position to end in the optic thalamus of the opposite side. The third neurone passes from the thalamus by the anterior limb of the internal capsule to the post-Rolandic cerebral cortex.

(*b*) *Spinotectal Fibres.*

The first neurone of this path also consists of the posterior root fibres that end in connection with Clarke's cells and posterior horn cells of the same side. The second neurone crosses to the opposite side and runs up in the antero-lateral position to end round the cells of the inferior corpora quadrigemina. The third neurone passes up through the internal capsule to end in the post-Rolandic cerebral cortex.

(*c*) *Indirect Cerebellar Fibres* (also known as ventro-spino-cerebellar).

Entering posterior root fibres arborise round cells of Clarke's column on the same side. From these cells fibres pass out to the antero-lateral position on the same side, and run up to pass to the cerebellar cortex by the superior peduncle.

It will be seen, therefore, that the connection between the periphery and the cerebral cortex is a contralateral or crossed one, and that between the periphery and the cerebellar cortex is ipsolateral or uncrossed.

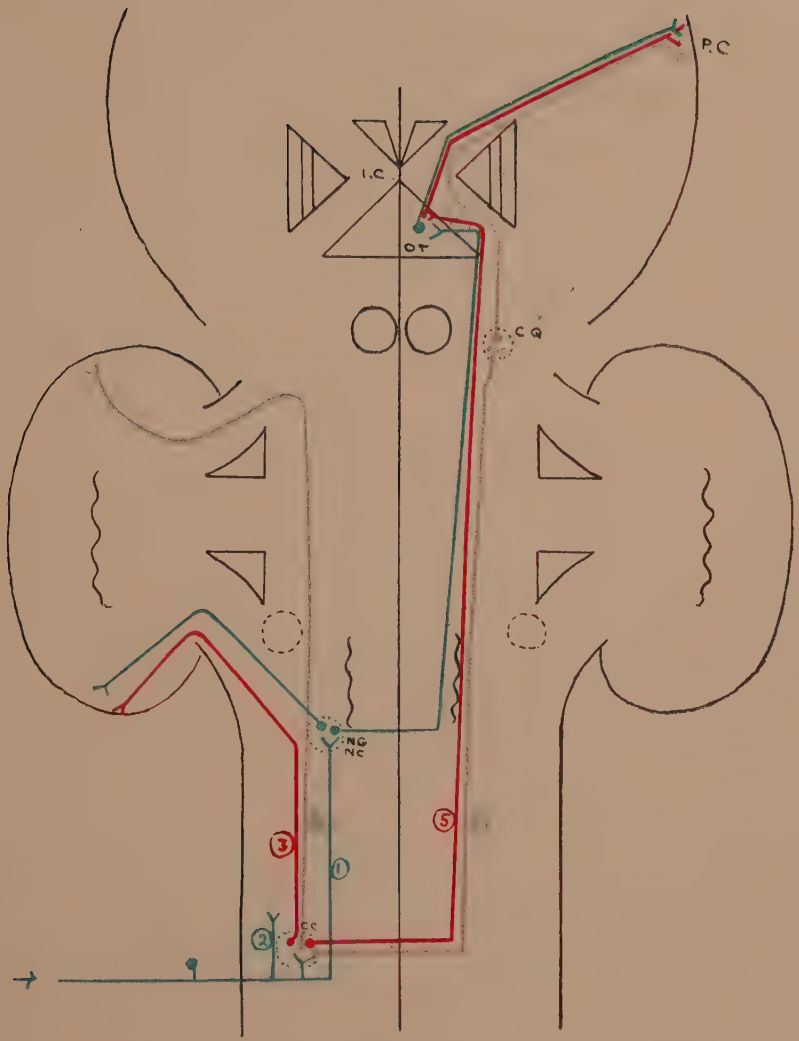

DIAGRAM 10.—Ascending Tracts of the Spinal Cord.

P.C. Post-Rolandic cerebral cortex.
O.T. Optic thalamus.
C.Q. Corpora quadrigemina.
N.G., N.C. Nuclei gracilis and cuneatus.
C.C. Clarke's cells.
I.C. Internal Capsule.

1. Columns of Goll and Burdach.
2. Tract of Lissauer.
3. Direct cerebellar tract.
4. Indirect cerebellar tract.
5. Spino-thalamic tract.
6. Spino-tectal tract.

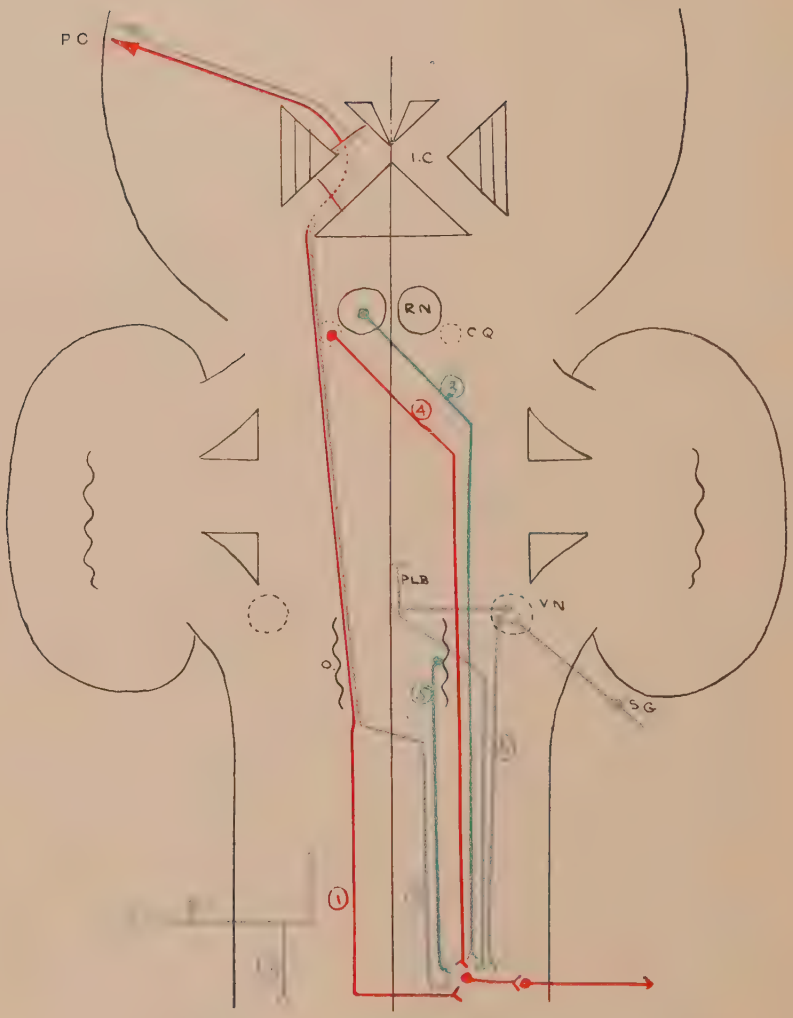

DIAGRAM 11.—Descending Tracts of the Spinal Cord.

P.C. Pre-Rolandic cerebral cortex.
I.C. Internal capsule.
R.N. Red nucleus.
C.Q. Corpora quadrigemina.
V.N. Vestibular nuclei.
S.G. Scarpa's ganglion.
P.L.B. Posterior longitudinal bundle.
O. Olive.

1. Direct pyramidal tract.
2. Crossed pyramidal tract.
3. Rubrospinal tract.
4. Tectospinal tract.
5. Olivospinal tract.
6. Vestibulospinal tract.
7. Comma tract.

CHAPTER IV

THE SPINAL CORD: DESCENDING TRACTS

THE fibres found descending in the spinal cord all terminate by turning into the central grey matter and arborising round cells there. A connector neurone carries the impulse to a cell in the anterior horn, and the axon of an anterior horn cell then passes out as an anterior root fibre to join a spinal nerve. These descending fibres originate in various higher centres, and run in definite groups or tracts in the cord (see Diagram 11).

1. DIRECT PYRAMIDAL TRACT (also known as column of Türck).

Pyramidal cells in the pre-Rolandic cerebral cortex (ascending parietal convolution) give rise to axons which pass down in the corona radiata, through the genu and anterior two-thirds of the posterior limb of the internal capsule, through the middle three-fifths of the crusta, through the pons, whose crossing fibres split up the pyramidal tracts into small bundles, through the medulla, where they appear as the pyramids on the anterior surface, to the cord; in the cord these fibres are found at the side of the anterior fissure. The fibres then cross in the anterior white commissure to end round cells of the opposite anterior horn. This tract does not extend below the thoracic region.

2. CROSSED PYRAMIDAL TRACT (also known as lateral pyramidal).

Fibres arise as axons of the pyramidal cells of the pre-Rolandic cerebral cortex, and follow the same path as the direct pyramidal fibres, running with them as far as the lower border of the medulla; here they cross over from the anterior position to the lateral position on the opposite side, cutting off the anterior horn of grey matter in so doing. (This grey matter then gives rise to the nucleus ambiguus and other motor nuclei of cranial nerves.) The fibres then run down the cord in the lateral position, ultimately turning in to connect with cells of the grey matter at various levels.

3. RUBROSPINAL TRACT (also known as pre-pyramidal or von Monakow's bundle).

Fibres arise as axons of cells in the red nucleus; they cross immediately to the opposite side anteriorly to the central canal as the decussation of Forel. They then pass down as a distinct tract to the spinal cord, where they are found immediately anterior to the crossed pyramidal tract. Ultimately the fibres turn in to connect with cells of the grey matter of the same side.

4. Tract of Lowenthal (also known as antero-lateral descending tract).

The fibres found descending in the antero-lateral region of the cord can be divided into three groups—tectospinal, olivospinal and vestibulospinal.

(*a*) *Tectospinal Fibres.*

Fibres arise from the superior corpora quadrigemina, cross to the opposite side in the decussation of Meynert anteriorly to the central canal, and pass out to the antero-lateral position; they then run down into the cord, and turn in to connect with cells of the grey matter of the same side.

(*b*) *Olivospinal Fibres.*

Fibres from the cells of the olivary nuclei also pass down to the cord in the antero-lateral position; some are crossed, and some uncrossed.

(*c*) *Vestibulospinal Fibres.*

These fibres are derived from the various vestibular nuclei of the same side. The details of these connections will be found in Part I., Chapter VI.

5. Comma Tract (also known as the tract of Schultze).

The incoming fibres of the posterior roots give off short descending branches, which run downwards in the cord for several segments before turning in to connect with posterior horn cells of the same side. (This tract thus corresponds to Lissauer's tract, which passes upwards.) The position of this tract varies at different levels in the cord, and receives in consequence different names:—

C. 1 to T. 10.—Comma tract, lying between columns of Goll and Burdach, deeply.

T. 10 to L. 3.—Septomarginal tract, lying next to the posterior septum.

L. 3 to S. 1.—Oval area of Flechsig, lying medially.

Sacral.—Posterior triangle of Gombault and Phillippe, most posteriorly.

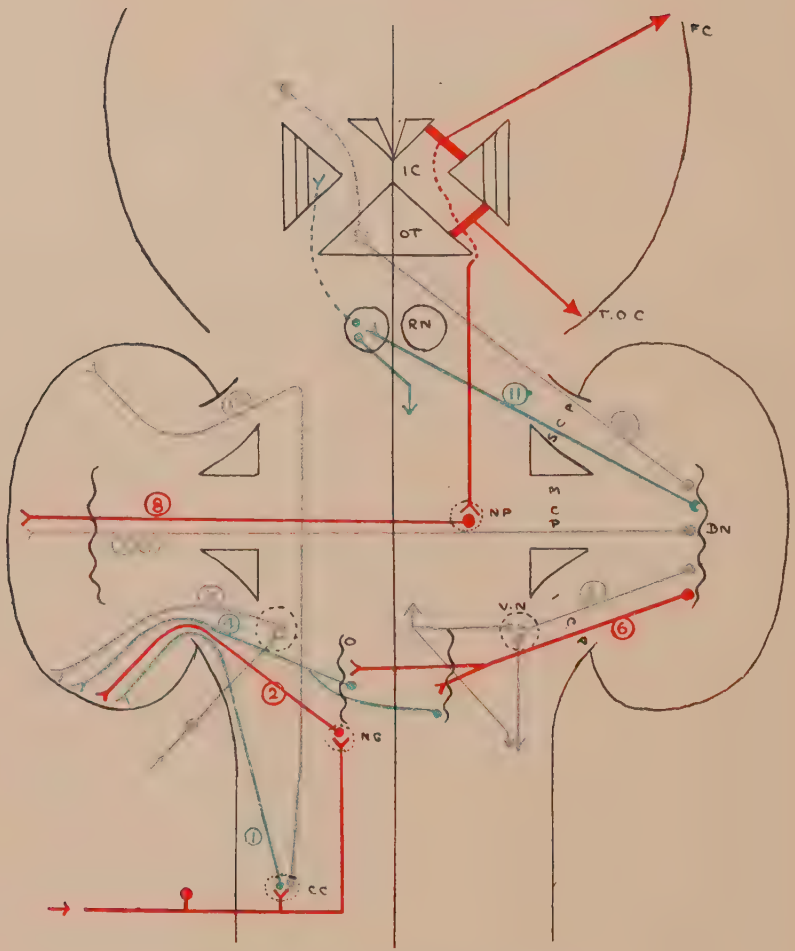

DIAGRAM 12.—Cerebellar Connections.

I.C. Internal capsule.
O.T. Optic thalamus.
F.C. Frontal cerebral cortex.
T.O.C. Temporal and occipital cortex.
R.N. Red nucleus.
S.C.P. Superior cerebellar peduncle.
M.C.P. Middle cerebellar peduncle.
I.C.P. Inferior cerebellar peduncle.
N.P. Nuclei pontis.
D.N. Dentate nucleus.
V.N. Vestibular nuclei.
O. Olive.
N.G. Nucleus gracilis.
C.C. Clarke's cells.

1. Direct cerebellar fibres.
2. External arcuate fibres.
3. Vestibular fibres.
4. Fibres from olives.
5. Fibres to vestibular nuclei.
6. Fibres to olives.
7, 9. Fibres from cerebellar nuclei of one side to opposite cerebellar cortex.
8. Fibres from nuclei pontis (cortico-pontine cerebellar).
10. Indirect cerebellar fibres.
11. Fibres to red nucleus.
12. Fibres to optic thalamus.

CHAPTER V

CEREBELLAR CONNECTIONS

The cerebellum receives impulses from all parts of the nervous system, the entering fibres passing straight to the cortex, where they arborise round the various cells present. The only exception to this rule is found in connection with the vestibular fibres, some of those that enter the cerebellum from Deiters' nucleus passing directly to the dentate nucleus. All the fibres that leave the cerebellum arise in the various nuclei, of which the dentate is the most important. The connection between the cortex and these nuclei is provided by the Purkinje cells ; the dendrites of these cells arborise in the outer layer of the cerebellar cortex, and their axons pass to the cerebellar nuclei ; the axons of the Purkinje cells never leave the cerebellum.

It is convenient to consider the cerebellar connections under the headings of entering and leaving fibres as found in the various cerebellar peduncles (see Diagram 12).

I. Inferior Cerebellar Peduncle (or restiform body).

A. **Entering Fibres.**

1. Direct cerebellar tract, from same side of cord.
2. External arcuate fibres, from nuclei gracilis and cuneatus of same side.
3. Vestibular fibres, from nuclei Deiters, Bechterew, and vestibular, of same side.
4. Olivary fibres, from olivary nuclei of both sides.

B. **Leaving Fibres.**

5. To Deiters' nucleus of same side, and thence relayed by
   (*a*) Vestibulo-spinal tract down cord.
   (*b*) Posterior longitudinal bundle up to nuclei of cranial nerves 6, 4, and 3.
6. To olives of both sides, and thence relayed by olivospinal tract down cord.

II. Middle Cerebellar Peduncle.

A. **Entering Fibres.**

7. From cerebellar nuclei of opposite side.
8. From pontine nuclei of opposite side (cortico-pontine-cerebellar tract).

B. **Leaving Fibres.**

9. To opposite cerebellar cortex.

(The crossing fibres of these three groups 7, 8, 9, cross ventrally in the pons.)

III. Superior Cerebellar Peduncle (or brachium conjunctivum).

A. **Entering Fibres.**

10. Indirect cerebellar tract, from same side of cord.

B. **Leaving Fibres.**

11. To opposite red nucleus, and thence relayed—

(*a*) To globus pallidus of same side.

(*b*) By rubrospinal tract to opposite side of cord.

12. To opposite optic thalamus, and thence relayed to cerebral cortex.

Thus the cerebellum is connected on both afferent and efferent sides with the same side of the cord, and with the opposite side of the cerebrum. It should be noticed also that in the superior cerebellar peduncles fibres entering the cerebellum are uncrossed, and those fibres leaving the cerebellum cross as the decussation of the superior peduncles anteriorly to the Sylvian aqueduct.

The connection between cerebellum and cerebrum is a crossed one, consisting, on both afferent and efferent paths, of two neurones (see Diagram 13).

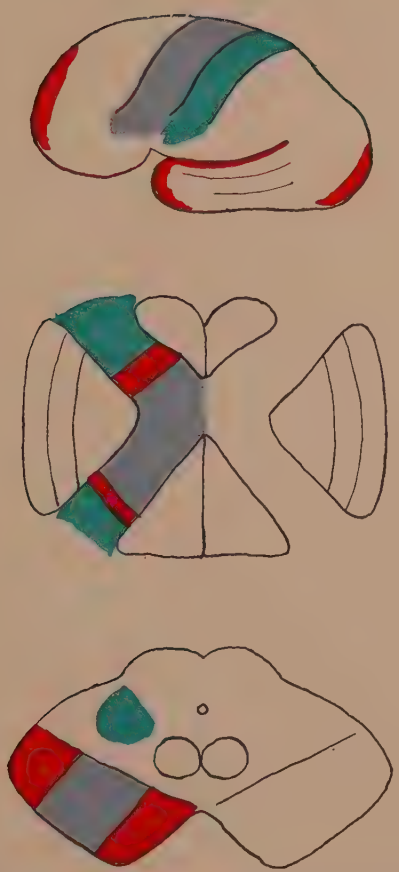

DIAGRAM 13.—Diagram to show Relative Positions of Important Fibres in Internal Capsule and Mid-brain.

Blue : Motor (pyramidal).
Red : Cortico-pontine cerebellar.
Green : Sensory (fillet group).

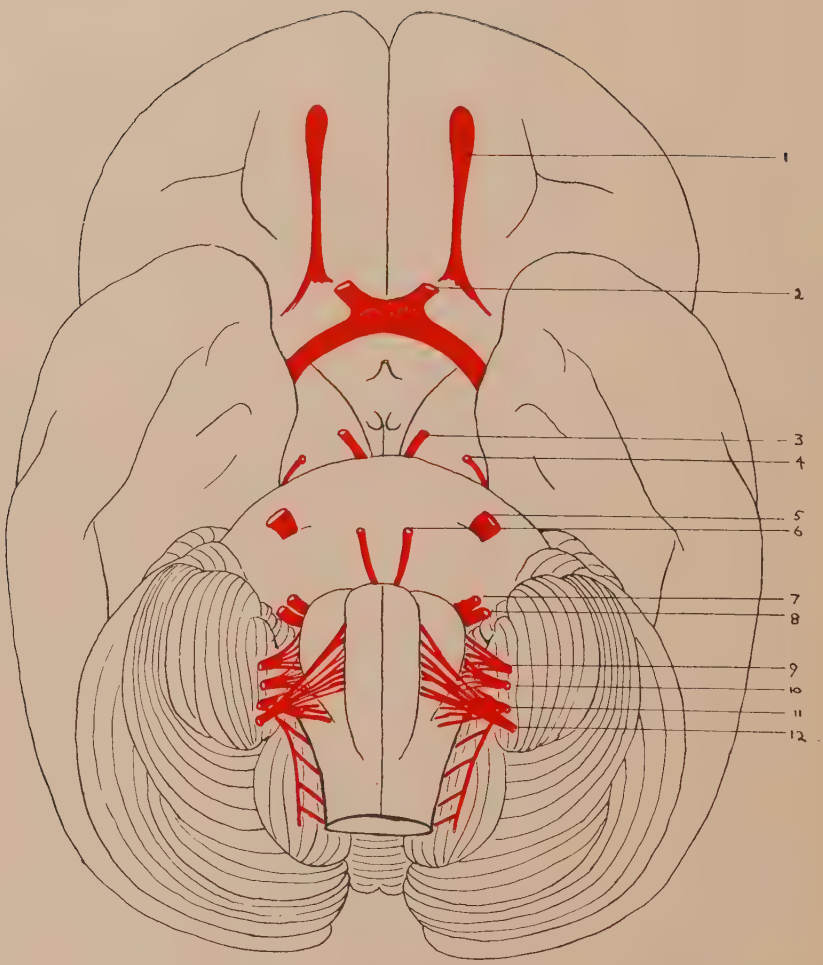

DIAGRAM 14.—Basal Aspect of Brain, showing Cranial Nerves.

CHAPTER VI

DEEP CONNECTIONS OF THE CRANIAL NERVES

By deep connections of the cranial nerves are meant the connections of these nerves within the brain substance. In spite of similar nomenclature, it is essential to distinguish between a *motor* nucleus and a *sensory* nucleus.

The *motor* nucleus of a cranial nerve consists of a group of nerve cells the axons of which pass outwards from the brain as the fibres of the motor nerve.

The *sensory* nucleus of a cranial nerve is made up of a group of cells around which arborise the incoming axons of cells which are found in some outlying ganglion. This outlying ganglion is the *true* nucleus of the sensory nerve, and the intracerebral " nucleus " is really a relay station on the path of the nerve. This station may relay impulses up to the cortex or downwards to the spinal cord.

The connection between the cerebral cortex and the motor nuclei is not in most cases definitely known. In the ensuing description mention is only made of the cortical connections where there is definite evidence of such paths.

It should be pointed out that the principal named nerve trunks and their branches are collections of a very great number of nerve fibres, and that it is possible for one " nerve " to contain fibres which have entirely different functions. In the process of branching the fibres devoted to a specialised function may leave the parent trunk, and pursue their path along another named nerve, while the rest of the fibres continue in the main pathway. Furthermore, certain specialised fibres may use a nerve pathway for a short distance and then pass on in the collection of fibres which compose another named nerve. This is well shown by the complicated course which the fibres conveying taste from the anterior part of the tongue pursue. These fibres use a series of pathways during their course from the tongue to the brain, and yet their function remains distinct throughout.

This shows clearly that a " physiological " nerve and an " anatomical " nerve are not by any means the same.

(See Diagram 14.)

CRANIAL NERVES

1. Olfactory (sensory).

Cells of Origin.—Special bipolar cells in nasal mucous membrane.

Axons.—Pierce cribriform plate of the ethmoid in twelve to fifteen bundles and enter the olfactory bulb, arborising round mitral cells in the bulb.

Secondary Neurone.—Arises in the bulb. The axons of mitral cells pass in the olfactory tract along the under-surface of the orbital portion of the frontal lobe in the olfactory sulcus to the tuberculum olfactarium and thence divide into a medial and lateral root.

(*a*) *Lateral root* passes directly outwards, curves medially again (over the island of Reil) and enters the pyriform lobe (uncus).

(*b*) *Medial root* passes medially upwards in the striæ of Lancisii, which are found lying on the corpus callosum in close association with the induseum griseum, which posteriorly reaches the fascia dentata. In man the striæ of Lancisii are the remnant of the hippocampal formation, and the induseum represents cells of the hippocampus (primitive smell cortex).

Tertiary Neurone.—Physiologically the tertiary neurones connect from the secondary centres—

1. *Viâ* the diagonal band of Broca.
2. Through fibres in the striæ terminalis back to the hypothalamus, epithalamus, and the ganglion habenulæ (these being known as the reflex centres).
3. To the hippocampal formation.[1]

From the *epithalamus* further connections are made with nuclei in the interpeduncular space, and thence to the tegmentum.

From the *hypothalamus* connections pass to the corpora mammillaria, and thence to the tegmentum and also to the anterior nucleus of the thalamus (see "Thalamic Nuclei Connections," Part I., Chapter VII.).*

(See Diagram 15.)

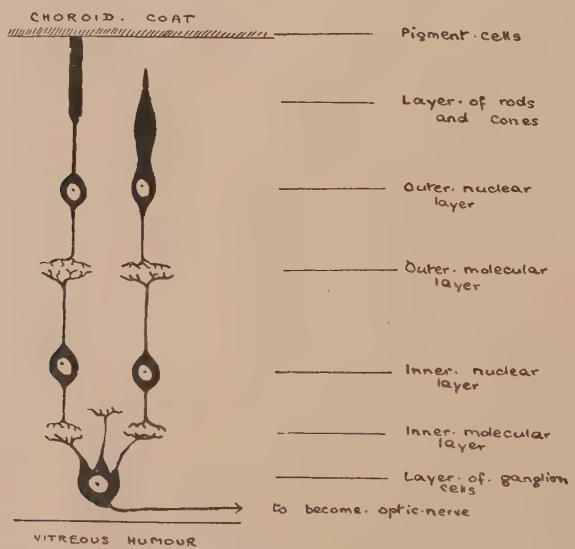

DIAGRAM 16.—Diagram showing neurone components of retina.

* This somewhat detailed anatomical description is given because of the intricate complication of the olfactory tract connections in the human brain, which has been so greatly modified in this respect.

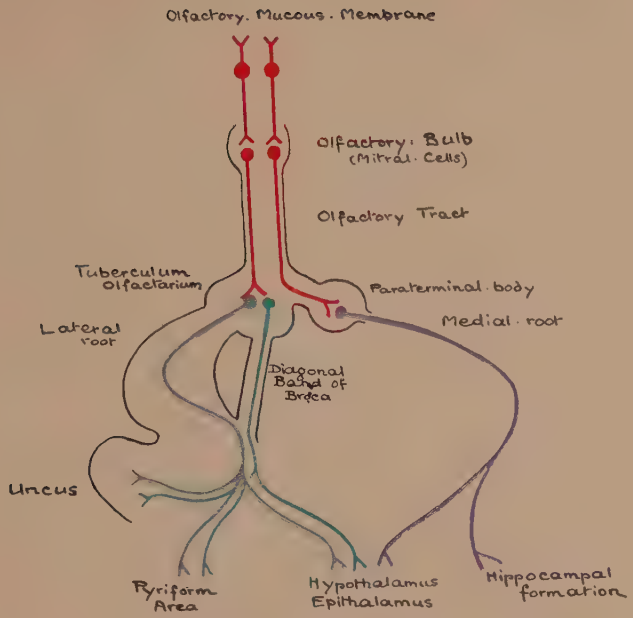

DIAGRAM 15.—Diagram of Olfactory Path.

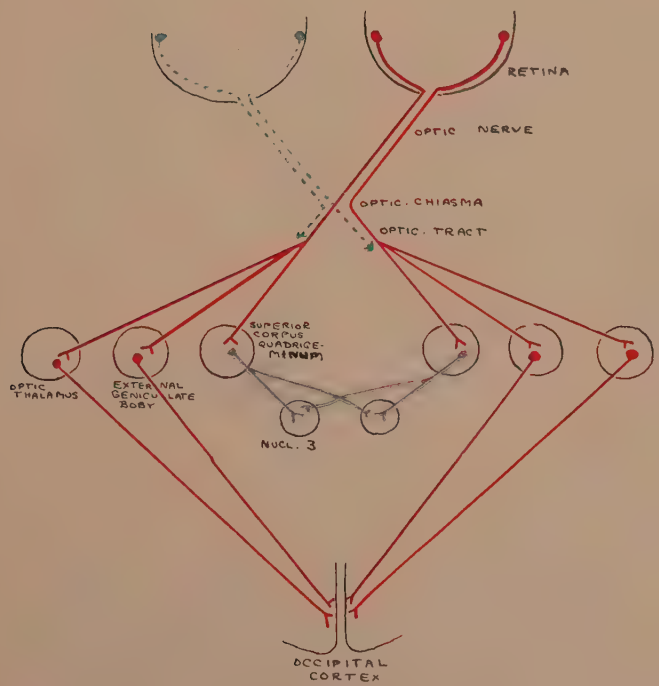

DIAGRAM 17.—Diagram to show the Optic Path.

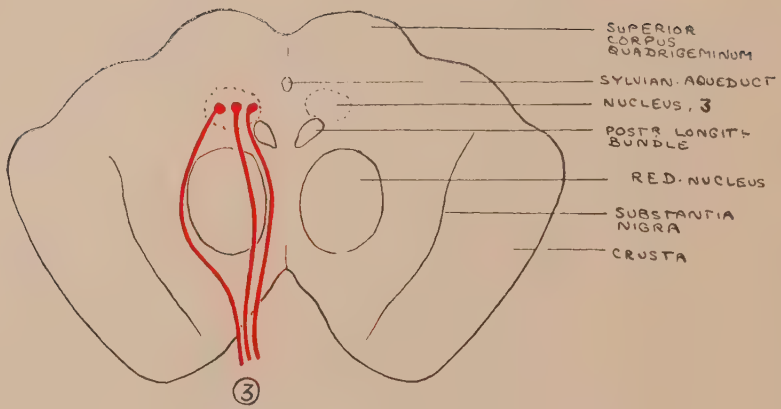

DIAGRAM 18.—Diagram to show Origin of Third Nerve.

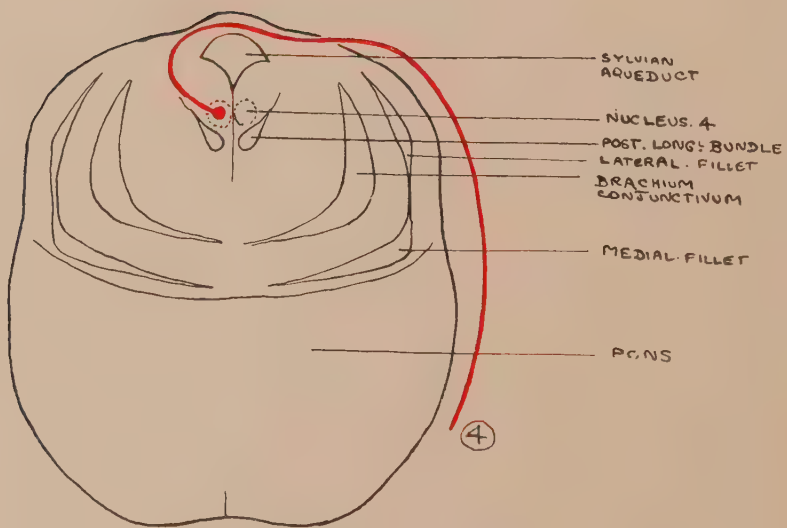

DIAGRAM 19.—Diagram to show Origin of Fourth Nerve.

2. Optic (sensory).

Cells of Origin.—Ganglion cells of the retina (see Diagram 16).

Axons.—Pass out of the eyeball as the optic nerve.

Fibres from the inner half of the retina cross in the optic chiasma, while those from the outer half continue on the same side. Thus the optic tract of one side contains—

(*a*) Fibres from the temporal half of the retina of that side.

(*b*) Fibres from the nasal half of the opposite retina.

(*c*) Fibres of Gudden's commissure.

(Gudden's commissure consists of fibres passing from the internal geniculate body of one side to the inferior corpus quadrigeminum of the other. According to some authorities, the fibres only link up the internal geniculate bodies of both sides. These fibres have nothing to do with the normal visual path.[2])

Visual fibres of the optic tract pass to—

(*a*) External geniculate body.

(*b*) Posterior nucleus of the thalamus.

(*c*) Superior corpus quadrigeminum.

These are known as the lower visual centres.

Secondary Neurone.—From the external geniculate body and the posterior nucleus of the thalamus to the occipital lobe of the cerebral cortex of the same side by means of the optic radiation. The macula is said to be bilaterally represented in the occipital cortex.[3]

(See Diagram 17.)

The superior corpus quadrigeminum is connected with the third nerve nucleus and thence to the ciliary ganglion (see " Interconnections of Cranial Nerves ").

3. Oculomotor (motor).

Cells of Origin.—Nucleus ventral to the Sylvian aqueduct, at level of the superior corpora quadrigemina. Nucleus consists of a *medial* part and of a pair of *lateral* nuclei.

Axons.—Emerge ventrally on the medial surface of the crura.

(See Diagram 18.)

In addition many afferent fibres (kinæsthetic from eye muscles) are found in the nerve, and their cells appear to lie on the trunk of the third nerve.

4. Trochlear (motor).

Cells of Origin.—Nucleus ventral to the Sylvian aqueduct, at level of the inferior corpora quadrigemina.

Axons.—Cross in the valve of Vieussens, emerge posteriorly, and curve round the crus of the opposite side.

(See Diagram 19.)

5. Trigeminal (mixed motor and sensory).

A. **Motor Part.**

Cells of Origin.

(α) Main motor nucleus. Upper pons.

(β) Accessory motor nucleus. Mid-brain. This is a long, narrow nucleus of unipolar cells extending from the superior corpora quadrigemina to the level of the main motor nucleus.

Axons.—Emerge at the side of the pons where the sensory fibres enter, and passing deep to the Gasserian ganglion, join the third (mandibular or inferior) division of the fifth nerve.

B. **Sensory Part.**

Cells of Origin.—Gasserian ganglion.

Axons.—Enter laterally at mid-pons and divide into an ascending and a descending branch.

(a) *Ascending Branch.*—Fibres arborise round cells constituting the sensory nucleus of the fifth nerve, lateral to the main motor nucleus.

(b) *Descending Branch.*—Fibres pass down as spinal (descending) root of the fifth nerve, giving off collaterals arborising round cells of the substantia gelatinosa of Rolando.

The substantia gelatinosa extends from this level to the level of the upper cervical cord (C_2), where it makes a cap of cells on the tip of the posterior horn.

Secondary Neurone.—Fibres from both these nuclei cross and run up as the trigeminal fillet (found lateral to the medial fillet) to the optic thalamus.

Tertiary Neurone.—Fibres from cells of the optic thalamus pass through the anterior part of the anterior limb of the internal capsule to the post-Rolandic cortex.

(See Diagram 20.)

6. Abducens (motor).

Cells of Origin.—Nucleus in floor of fourth ventricle near the mid-line, directly deep to the arching fibres of the seventh nerve, which make the elevation in the floor of the ventricle known as the eminentia teres (colliculus facialis).

Axons.—Pass out to emerge near the mid-line on the ventral surface at the lower border of the pons.

(See Diagram 21.)

7. Facial (motor and sensory). (Sensory part is the nervus intermedius of Wrisberg.)

A. **Motor Part.**

Cells of Origin.—Ventro-lateral in lower pons.

(See Diagram 22.)

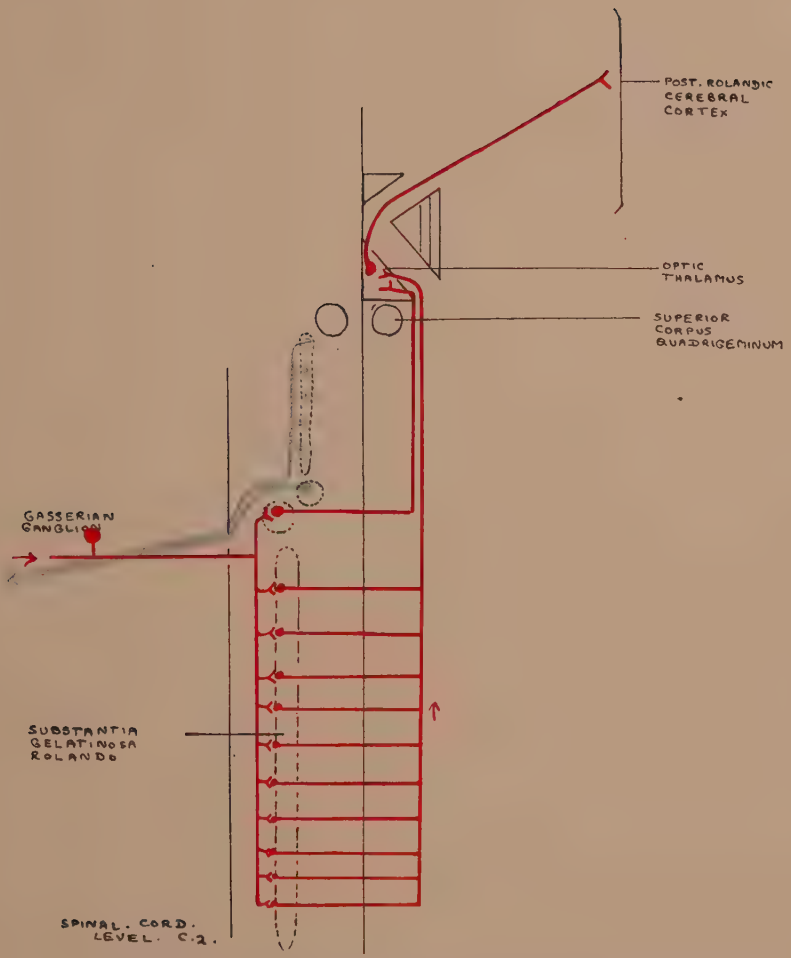

DIAGRAM 20.—Diagram of Path of Fifth Nerve Fibres in the Brain.
Red: Sensory. Blue: Motor.

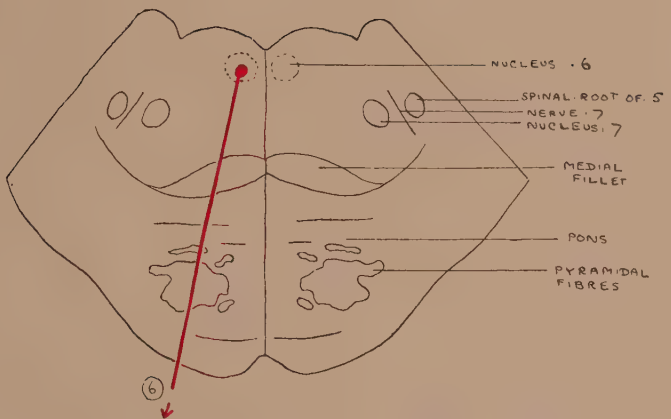

DIAGRAM 21.—Diagram to show Origin of Sixth Nerve.

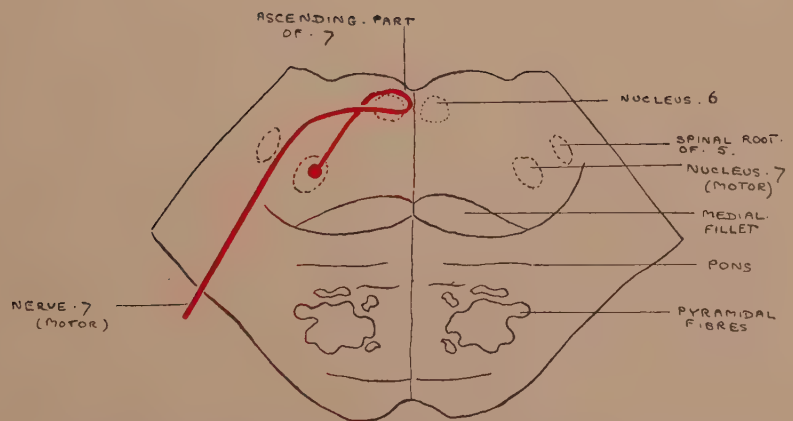

DIAGRAM 22.—Diagram to show Origin of Motor Part of Seventh Nerve.

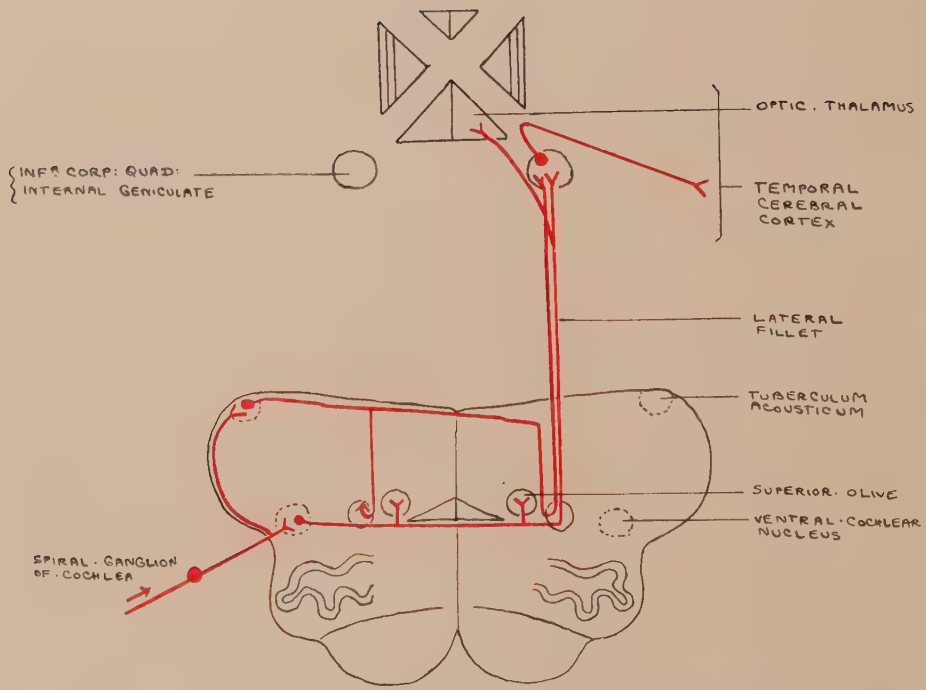

DIAGRAM 23.—Diagram to show Path of Fibres of Cochlear Division of Eighth Nerve.

(N.B.—These cells receive connections from motor cerebral cortex of both sides.)

Axons.—Pass backwards towards the mid-line and arch over the nucleus of the sixth nerve, making the rounded elevation on the floor of the fourth ventricle (eminentia teres or colliculus facialis). The fibres then emerge ventrally, passing between the nucleus of the seventh nerve and the substantia gelatinosa and appearing at the inferior border of the pons.

B. **Sensory Part.**

Cells of Origin.—Geniculate ganglion.

Dendrites.—Are carried in the chorda tympani and great superficial petrosal nerves to the ganglion.

Axons.—Pass as the nervus intermedius of Wrisberg to enter the pons at the same point at which the motor part of the seventh nerve emerges and the eighth nerve enters the brain; they then pass to the superior part of the column of grey matter in connection with the tractus solitarius.

Secondary Neurone.—Fibres cross, and join the medial fillet running to the optic thalamus.

Tertiary Neurone.—From the thalamus the fibres pass to the hippocampal gyrus.

The *Glossopalatine* nerve is the name given to the nervus intermedius (sensory 7), the geniculate ganglion, and the great superficial petrosal and chorda tympani nerves, which are both sensory and motor. This is quite apart from the motor fibres of 7 which supply the facial muscles. The central connections and peripheral distribution of this nerve resemble those of the ninth nerve, and suggest it being considered as an aberrant part of the latter.[4]

8. Auditory or Acoustic (sensory).

This consists of two parts :—

1. Cochlear.
2. Vestibular.

Cochlear Nerve.

Cells of Origin.—Bipolar cells in the spiral ganglion of the cochlea.

Dendrites.—Arborise among the hair cells of the organ of Corti.

Axons.—Enter at the lower border of the pons. The fibres then divide and pass to—

(*a*) Ventral cochlear nucleus.

(*b*) Dorsal cochlear nucleus or tuberculum acousticum.

(See Diagram 23.)

Secondary Neurone.

(*a*) From the ventral nucleus some fibres cross as the trapezoid fibres and then turn up as the lateral fillet of the opposite side, passing

to the inferior corpus quadrigeminum and internal geniculate body of the thalamic region, while other fibres join the lateral fillet on the same side.

(Some fibres connect with superior olives on *both* sides.)

(*b*) From the dorsal nucleus some fibres cross as the striæ acousticæ (striæ medullares) in the floor of the fourth ventricle, and in the mid-line turn deeply, and join the fibres from the ventral nucleus in the lateral fillet. Other fibres join the lateral fillet on the same side.

Tertiary Neurone.—Fibres pass from the internal geniculate body and the inferior corpus quadrigeminum through the auditory radiation to the temporal cortex (especially the posterior third of the superior temporal convolution).

(Some American writers consider that the last auditory neurone is from the internal geniculate body only to the cortex, thus making the internal geniculate body into a lower auditory centre. The inferior corpus quadrigeminum is regarded merely as a reflex centre for co-ordinating eye and body movements with auditory impressions, while the optic thalamus is not regarded as a cell station on the auditory path.[5])

Vestibular Nerve.

Cells of Origin.—In Scarpa's ganglion.

Dendrites.—Come from cristæ and maculæ of vestibular part of the inner ear.

Axons.—Enter the low border of the pons and divide into an ascending and a descending branch.

Descending Branch (Roller's bundle).—These fibres end within the nucleus nervi vestibularis spinalis, which extends as far as the posterior column nuclei.

Ascending Branch.—Divides into three, passing to—

(*a*) Principal vestibular nucleus (dorsal nucleus).

(*b*) Deiters' nucleus (lateral nucleus).

(*c*) Bechterew's nucleus (superior nucleus).

Secondary Neurone.—From these three nuclei fibres pass to the cerebellar cortex by the inferior cerebellar peduncles. A few pass direct to the cerebellar nuclei.

(See Diagram 24.)

Further Connections.

(1) From the principal vestibular nucleus fibres pass antero-laterally and then down the cord as part of the vestibulospinal tract.

(2) From Deiters' nucleus fibres pass to the mid-line and divide into descending and ascending branches.

(*a*) The descending branch passes antero-laterally, and joins the vestibulospinal tract of the cord (anterior fasciculus proprius or ground bundle).

(*b*) The ascending branch passes upwards as part of the posterior

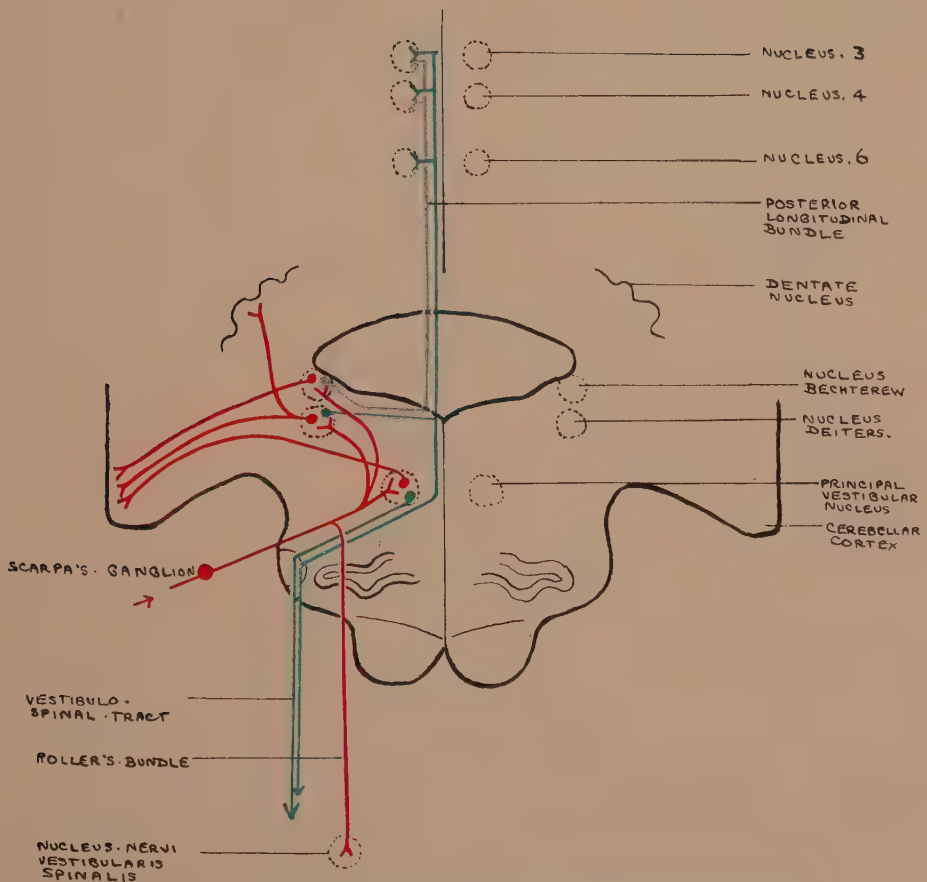

DIAGRAM 24.—Diagram to show Path of Vestibular Fibres of Eighth Nerve.

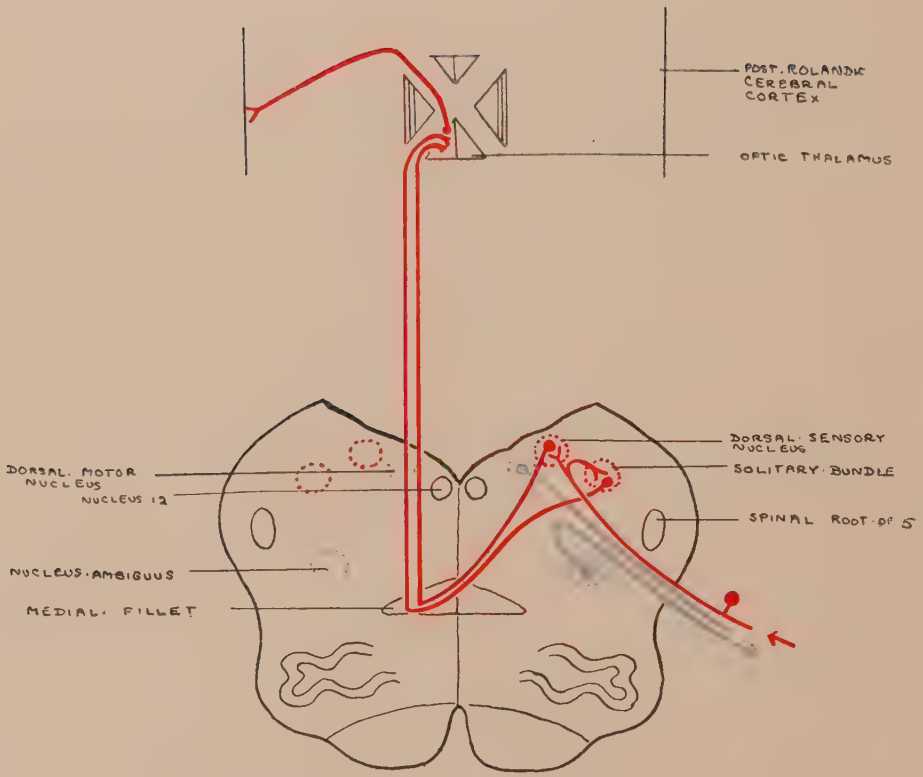

DIAGRAM 25.—Diagram to show Cranial Path of Nerves 9 and 10.
Red : Sensory. Blue : Motor.

longitudinal bundle, giving off collaterals to the nuclei of cranial nerves 6, 4, and 3.

(3) From Bechterew's nucleus fibres pass to the nuclei of cranial nerves 4 and 3 direct.

(According to Muskens, the vestibular nuclei are also connected with the corpus striatum by fibres that cross in the posterior commissure.[6])

9. Glossopharyngeal (motor and sensory).

Motor.

Cells of Origin.

(*a*) Principal (dorsal) nucleus in the floor of the fourth ventricle lateral to the vagal motor nucleus. (This nucleus supplies parasympathetic fibres.)

(*b*) Nucleus ambiguus (ventral), lying anterior to the principal nucleus. (This ventral nucleus supplies fibres to voluntary muscles.)

(N.B.—The nucleus ambiguus represents anterior horn cells cut off by the decussation of the crossed pyramidal tract.)

Axons.—From both nuclei emerge between the olive and the restiform body.

Sensory.

Cells of Origin.—Jugular and petrosal ganglia.

Axons.—Enter between restiform body and olive and divide into ascending and descending branches.

Ascending branches end in the dorsal or principal sensory nucleus.

Descending branches join solitary bundle, and end round these cells. (These fibres carry taste sense.)

Secondary Neurone.—Fibres arising in these two nuclei cross the middle line, and pass up with the medial fillet to the optic thalamus.

Tertiary Neurone.—From the optic thalamus to the cerebral cortex.

(See Diagram 25.)

10. Vagus (motor and sensory).

Motor.

Cells of Origin.

(*a*) Principal (dorsal) nucleus in the floor of the fourth ventricle lying lateral to the twelfth nucleus. The corresponding area in the floor of the ventricle is known as the ala cinerea or trigonum vagi. This nucleus also supplies parasympathetic fibres.

(*b*) Nucleus ambiguus (ventral) lying anterior to the principal nucleus. The nucleus ambiguus supplies fibres to voluntary muscles.

Axons.—From both nuclei emerge between the olive and the restiform body.

Sensory.

Cells of Origin.—Ganglia of the root and trunk of the vagus.

Axons.—Enter between the restiform body and the olive and divide into ascending and descending branches.

Ascending branches end in the dorsal or principal sensory nucleus.

Descending branches join the solitary bundle, ending round cells in that region.

Secondary neurone and *tertiary neurones* are the same as for the glossopharyngeal nerve; *i.e.*, the fibres cross the middle line and pass up with the medial fillet to the thalamus, and thence to the cerebral cortex.

(See Diagram 25.)

11. Spinal Accessory.

This nerve consists of two parts :—

(1) Spinal part, which is motor.

(2) Accessory part, which is motor and is so called because it is "accessory" to the vagus.

Spinal Part.

Cells of Origin.—Anterior horn cells of the first five cervical segments.

Axons.—Emerge laterally from the cord, and joining together run up in the spinal canal and then join the accessory part of the eleventh nerve. (Some fibres arise from the upper two or three cervical roots, join the vagus nerve trunk, and are distributed with it to involuntary structures. These are the parasympathetic fibres.)

Accessory Part.

Cells of Origin.—The same column of cells which higher up constitutes the nucleus ambiguus.

Axons.—Emerge between the olive and the restiform body and join the vagus trunk.

(See Diagram 26.)

12. Hypoglossal (motor).

Cells of Origin.—Nucleus near the mid-line in the floor of the fourth ventricle, extending throughout the medulla. The upper part is subjacent to the trigonum hypoglossi.

Axons.—Emerge between the pyramid and the olive.

(See Diagram 26.)

INTERCONNECTIONS OF THE CRANIAL NERVES

Certain of the cranial nerves make connections with other cranial nerve nuclei within the substance of the brain itself. It is essential for the clear understanding of the effect of local and multiple lesions that the more important of these connections should be noted.

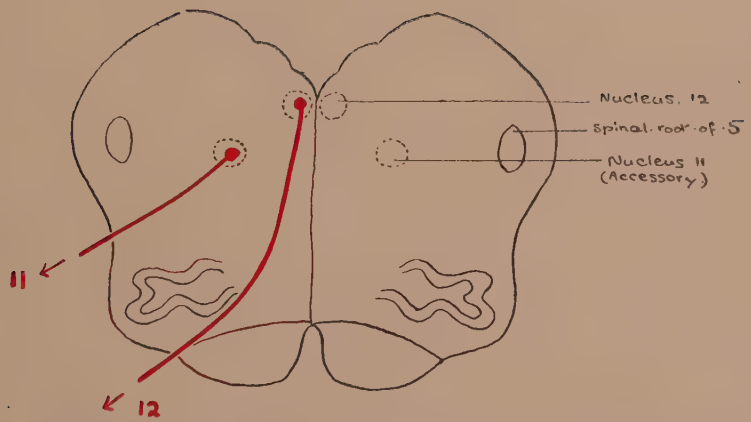

DIAGRAM 26.—Diagram to show Origin of Nerves 11 (accessory part) and 12.

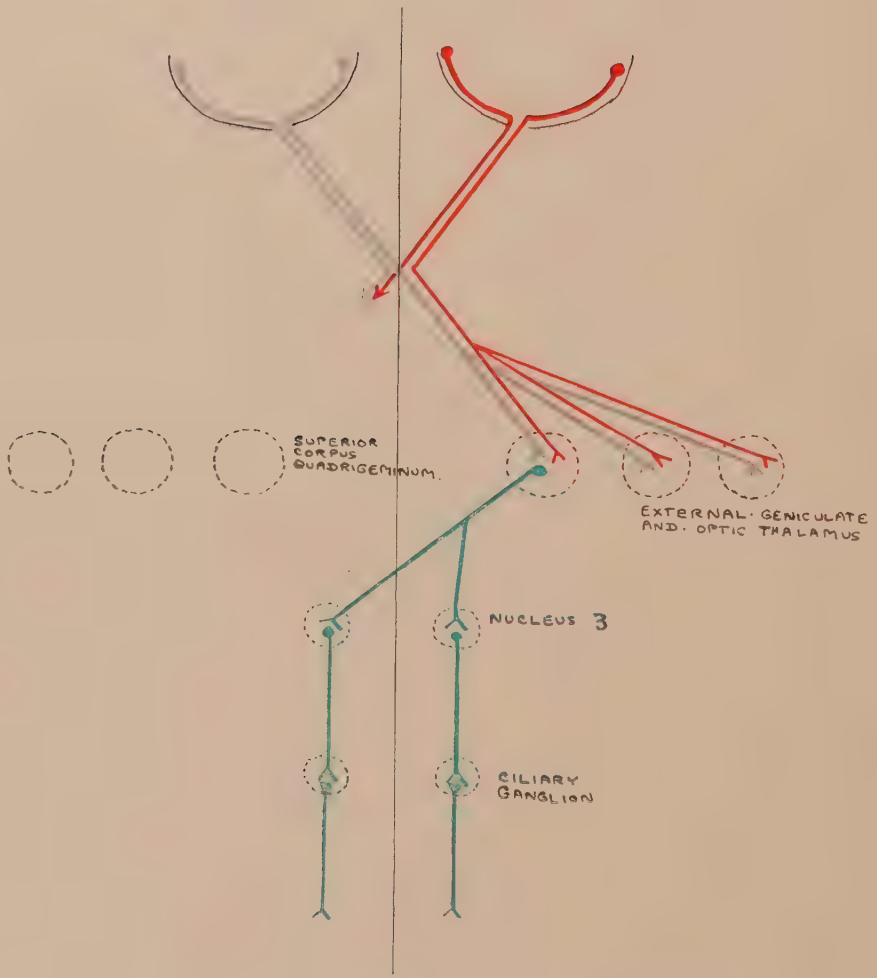

DIAGRAM 27.—Diagram to show Connection of Optic Nerve with the Oculomotor Nerve.

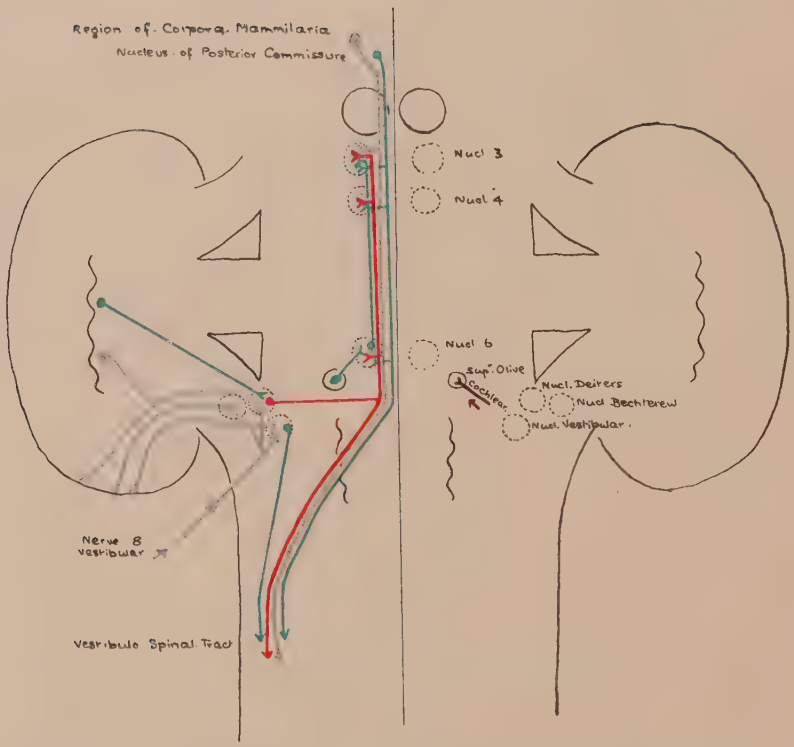

DIAGRAM 28.—Diagram to show Fibres of Posterior Longitudinal Bundle.

A. **Connections of the Optic Nerve with the Oculomotor Nerve.**

Fibres from the optic tract, containing fibres from both eyes, relay through the superior corpus quadrigeminum to the nucleus of the opposite oculomotor nerve, crossing partly in the posterior commissure of the brain. From this oculomotor nucleus fibres pass to the ciliary ganglion and thence (as post-ganglionic fibres) to the constrictor pupillæ muscle *viâ* the short ciliary nerves.

(See Diagram 27.)

B. **Connections of the Oculomotor Nerve with the Trochlear, Abducens, Vestibular and Cochlear Nerves.**

The most important band of fibres in this connection is the posterior longitudinal bundle (also known as the medial longitudinal bundle and the fasciculus longitudinalis medialis). This band consists of the following fibres, which are all uncrossed connections :—

(*a*) Fibres from Deiters' nucleus (vestibular 8) which run to the mid-line and divide into—

1. A descending branch that joins the vestibulospinal tract in the cord ;
2. An ascending branch that gives off collaterals to the nuclei of the abducens, trochlear and oculomotor nerves, and ends in the mid-brain.

(*b*) Fibres from the abducens nucleus to the oculomotor nucleus.

(*c*) Fibres from a nucleus just behind the corpora mammillaria, and from the nucleus of the posterior commissure, passing down giving off collaterals to the nuclei of the abducens, trochlear and oculomotor nerves and joining the vestibulospinal tract.

(See Diagram 28.)

In addition there are fibres from the superior olive (which itself receives fibres from cochlear 8) that pass to the abducens nucleus, and thence connect with the nucleus of the third nerve by the posterior longitudinal bundle.

(It should be noted that the descending fibres which subsequently join the vestibulospinal tract, together with other fibres from the inferior and superior corpora quadrigemina, are called by some writers the tectospinal tract.)

C. **Connections of the Facial Nerve with the Trigeminal and the Glosso-pharyngeal Nerves.**

(*a*) With the Trigeminal Nerve.

(i.) *Sensory Division of the Fifth Nerve.*

(*a*) Fibres from Meckel's (spheno-palatine) ganglion pass *viâ* the superior maxillary nerve and the Gasserian ganglion to the nucleus of the sensory part of the fifth nerve.

(*Meckel's ganglion* also receives secretomotor fibres from the facial nerve arising from its motor nucleus and passing through the geniculate ganglion, and then as the great superficial petrosal nerve to join the great deep petrosal nerve,

making the Vidian nerve. The great deep petrosal contains post-ganglionic fibres, and is derived from the plexus round the internal carotid artery.)

(β) Fibres of the fifth nerve, carrying taste from the anterior two-thirds of the tongue, run in the lingual nerve with sensory fibres of the facial. The latter join the chorda tympani nerve, passing *viâ* the geniculate ganglion and the nervous intermedius of Wrisberg to the dorsal sensory nucleus of the facial nerve. The fibres of the trigeminal then pass on to the Gasserian ganglion *viâ* the mandibular division, and thence to the sensory nucleus of the fifth nerve.

(γ) Fibres from the spinal (sensory) root of the fifth nerve make connection with the motor nucleus of the facial.

(ii.) *Motor Division of the Fifth Nerve.*

Fibres from the motor nucleus of the fifth nerve pass out along the third or mandibular division of the fifth to the otic ganglion.

(*Otic ganglion* also receives post-ganglionic sympathetic fibres from the plexus round the middle meningeal artery, and gives rise to sensory fibres in the lesser superficial petrosal nerve. This lesser superficial petrosal nerve is made by—

(*a*) Fibres passing from the otic ganglion *viâ* the tympanic plexus in the tympanic branch of the glossopharyngeal nerve (known as Jacobsen's nerve) to the petrous ganglion and thence to the solitary bundle.

(*b*) Fibres passing from the otic ganglion to the geniculate ganglion either directly or through the tympanic plexus, and thence by the nervus intermedius to the dorsal sensory nucleus of the facial nerve. This dorsal sensory nucleus of the facial is continuous in the brain stem with the solitary bundle, which is itself the accessory sensory nucleus of the glossopharyngeal and vagus nerves.)

(*b*) With the Glossopharyngeal Nerve.

(i.) *Sensory Division of the Ninth Nerve.*

(α) Fibres from the posterior third of the tongue, carrying taste, pass in the main ninth nerve trunk *viâ* the petrous ganglion to the solitary bundle, which, as previously described, is continuous with the dorsal sensory nucleus of the facial.

(β) Fibres from the otic ganglion (which also gives rise to the sensory fibres of the facial) pass *viâ* the tympanic plexus (see above) to the petrous ganglion and thence to the solitary bundle.

(ii.) *Motor Division of the Ninth Nerve.*

Fibres from the main motor nucleus of the glossopharyngeal nerve pass to the otic ganglion by the tympanic nerve and the lesser

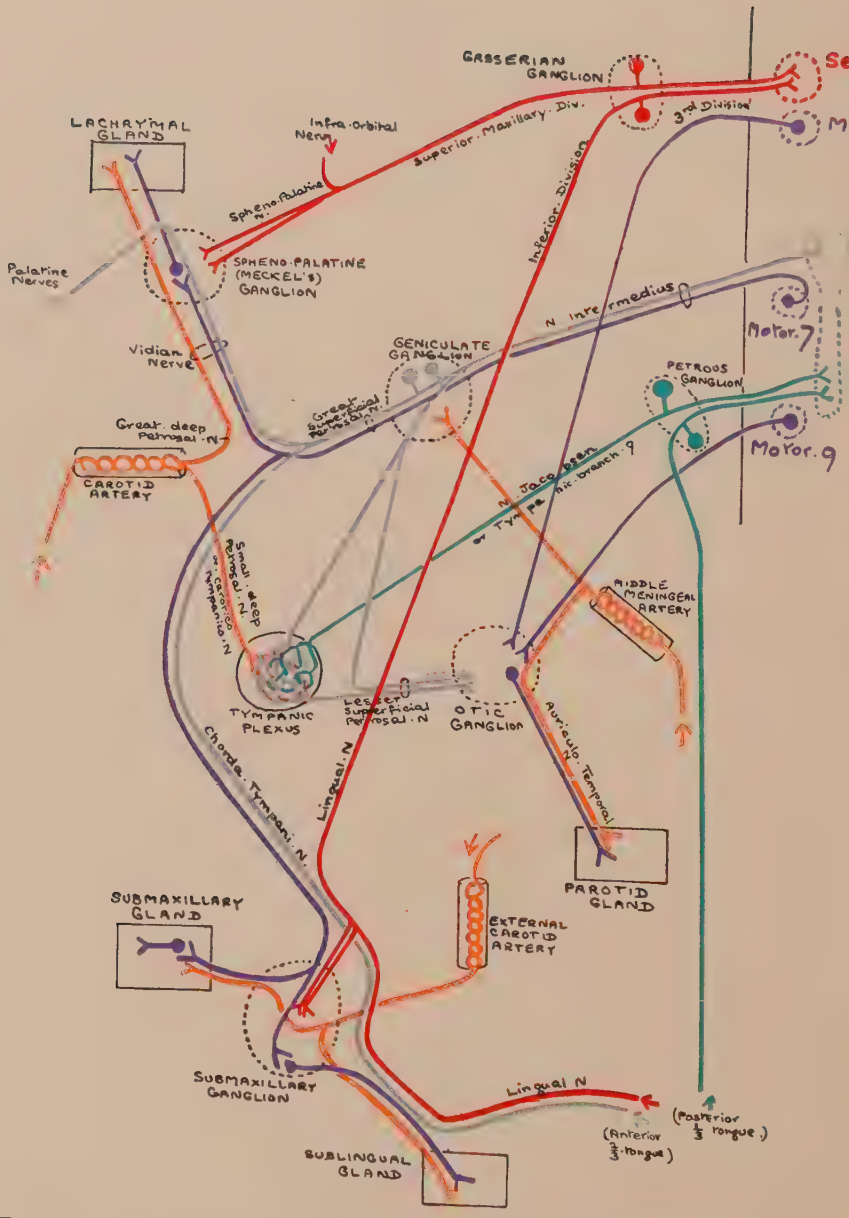

DIAGRAM 29.—Diagram to show Innervation of Salivary and Lachrymal Glands.

Red : Sensory 5. Green : Sensory 9.
Blue : Sensory 7. Purple : Motor (parasympathetic) 5, 7, 9.
Orange : Sympathetic (post-ganglionic).

superficial petrosal nerves, which must therefore be regarded as mixed nerves.

(*c*) With the Submaxillary Ganglion.

(i.) The motor root to the ganglion comes from the seventh nerve *viâ* chorda tympani. The fibres to the submaxillary gland pass right through the ganglion, while those to the sublingual gland have a cell station in the ganglion.

(ii.) Sensory fibres arise in the ganglion and pass *viâ* the lingual nerve to the Gasserian ganglion, and thence to the sensory nucleus of the fifth nerve.

(iii.) Sympathetic (post-ganglionic) fibres come from the plexuses around the external carotid and facial arteries, passing through the ganglion to the submaxillary and sublingual glands.

(*d*) The Motor Nucleus of the Facial Nerve.

This has further connections with—

(i.) The spinal root of the fifth nerve (sensory), receiving from thence most of its afferent impulses.

(ii.) The corpus trapezoideum.

(iii.) The pyramidal tract of the opposite side.

D. Innervation of the Lachrymal and Salivary Glands.

(*a*) The Lachrymal Gland.

1. *Secretomotor* fibres from the facial nerve, having a cell station in Meckel's ganglion.
2. *Sympathetic* fibres (post-ganglionic) from the upper part of the sympathetic chain make a plexus on the internal carotid artery and pass thence by the great deep petrosal nerve and the Vidian nerve through Meckel's ganglion to the gland.

(*b*) The Submaxillary Gland.

1. *Secretomotor* fibres from the facial nerve *viâ* the chorda tympani, having a cell station in the submaxillary gland.
2. *Sympathetic* fibres (post-ganglionic) from the upper part of the sympathetic chain make a plexus on the external carotid and facial arteries, and pass from there through the submaxillary ganglion to the gland.

(*c*) The Sublingual Gland.

1. *Secretomotor* fibres from the facial nerve *viâ* the chorda tympani, having a cell station in the submaxillary ganglion.
2. *Sympathetic* fibres (post-ganglionic) are the same as for the submaxillary gland, and pass through the submaxillary ganglion to the gland.

(*d*) The Parotid Gland.

1. *Secretomotor* fibres from the fifth and ninth nerves, having a cell

station in the otic ganglion, the fibres passing from there in the auriculo-temporal nerve to the gland.

2. *Sympathetic* fibres (post-ganglionic) from the (*a*) plexus on the external carotid artery; (*b*) plexus on the middle meningeal artery, through the otic ganglion and thence in the auriculo-temporal nerve.

(See Diagram 29.)

E. Relations between the Tenth and the Eleventh Nerves.

The *spinal* part of the eleventh nerve supplies the sternomastoid and the trapezius muscles, while the *accessory* (cerebral) part of the nerve joins the vagus, and through the external and recurrent laryngeal nerves supplies the muscles of the larynx. The greater part of the motor fibres of the vagus are in reality derived from the accessory part of the eleventh nerve (" accessory " signifying accessory to the vagus). This will include the pre-ganglionic motor fibres to the heart and alimentary canal.

F. Summary of the Tracts conveyed in the Fillets.

I. *Medial Fillet.*

1. Fibres from the opposite nucleus gracilis and nucleus cuneatus, passing up to the optic thalamus.
2. Fibres of the spinothalamic and spinotectal tracts join the fillet.
3. Fibres from the nuclei of the sensory cranial nerves (10, 9 and 7).

II. *Lateral Fillet.*

Fibres from both cochlear nuclei and from the superior olives, chiefly of the opposite side, passing up to the inferior corpus quadrigeminum and the internal geniculate body.

III. *Trigeminal Fillet.*

Fibres from both sensory nuclei of the fifth nerve of the opposite side. In the mid-brain this fillet is indistinguishable from the medial fillet.

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[3] Hartridge in Starling's " Principles of Human Physiology," 3rd ed., p. 552.
[4] Whitnall in Cunningham's " Text-book of Anatomy," 1922, p. 695.
[5] Keiller. " Anatomy and Physiology of the Nerve Tracts of the Brain and Cord." 1927. (Macmillan.)
[6] Muskens. *Brain*, 1922, Vol. XLV., p. 454.

CHAPTER VII

BASAL GANGLIA CONNECTIONS

THE term " basal ganglia " is taken to include the

Optic thalamus

Corpus striatum { Caudate nucleus. / Lenticular nucleus (putamen and globus pallidus).

Amygdaloid nucleus.

Claustrum.

Of these nuclei the optic thalamus is the oldest sensory centre, and is not included in the term " corpus striatum " which is motor in function. This distinction in function is borne out by the differences in the cell types present. The optic thalamus cells are of sensory type, comparatively small and multipolar, and including many of the extremely branched connector cells known as Golgi type II. The globus pallidus contains large multipolar cells of typical motor form, while the caudate nucleus and putamen consist of smaller similar cells with short axons passing only to the globus pallidus.

The developmental significance and functions of these nuclei will be discussed in Part II., Chapter VI., but the meaning of their various connections will be understood more readily if it is remembered that the optic thalamus is the most important receiving station on the sensory path, that the globus pallidus is developed from the palæostriatum and represents the oldest motor cortex, and that the caudate nucleus and putamen are developed later from the neostriatum and represent a refining influence exerted on the globus pallidus motor activities by linking up this nucleus with the thalamus.

(See Diagram 30.)

Basal Ganglia Connections.

A. Fibres coming from elsewhere, and ending in the basal ganglia :—

(i.) To thalamus by all sensory paths.
(ii.) To thalamus from contralateral cerebellar nuclei.
(iii.) To thalamus from corpora mammillaria.
(iv.) To thalamus from ipsolateral cerebral cortex.
(v.) To globus pallidus from red nucleus of same side (and thus from cerebellum of opposite side).

B. Fibres arising and ending within the basal ganglia :—

(i.) From thalamus to caudate nucleus.
(ii.) From thalamus to globus pallidus.
(iii.) From caudate nucleus to putamen.
(iv.) From caudate nucleus to globus pallidus.
(v.) From putamen to globus pallidus.
(vi.) From globus pallidus to thalamus.

C. Fibres arising in the basal ganglia and ending elsewhere :—

(i.) From globus pallidus to ipsolateral red nucleus and thence relayed by rubrospinal tract to opposite side of cord.

(ii.) From globus pallidus to ipsolateral substantia nigra, and thence relayed to accessory motor nucleus of 5.

(See Diagram 31.)

The Internal Capsule.

This consists of a band of white matter semilunar in shape with its convexity directed medially. The anterior division (or limb) lies between the caudate and lenticular nuclei, the posterior division lying between the optic thala-

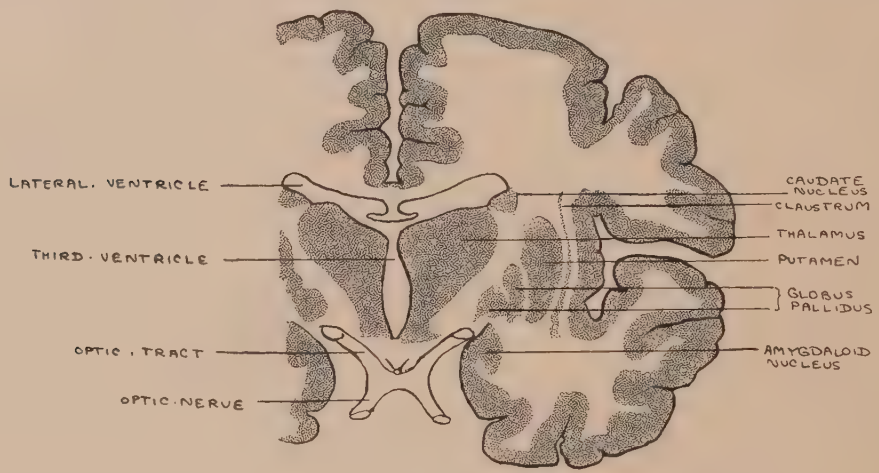

DIAGRAM 30.—Diagram to show basal ganglia. (*After Cunningham.*)

mus and lenticular nucleus ; the two limbs form together a knee-shaped bend, which is known as the middle division or genu.

The fibres found in the internal capsule are as follows :—

(*a*) *Anterior Limb.*

(i.) Last neurone on sensory path to frontal and parietal cerebral cortex.

(ii.) Fronto-pontine-cerebellar fibres, from frontal cortex to nuclei pontis and thence relayed to opposite cerebellar cortex.

(iii.) Corticothalamic fibres, from cerebral cortex to thalamus.

These three groups of fibres constitute the corona radiata.

(*b*) *Genu.*

(i.) Some of the motor fibres from the pre-Rolandic cerebral cortex.

(*c*) *Posterior Limb.*

(i.) Remainder of the motor fibres from the pre-Rolandic cerebral cortex.

(ii.) Fibres from pre-Rolandic cerebral cortex to red nucleus (Monakow).

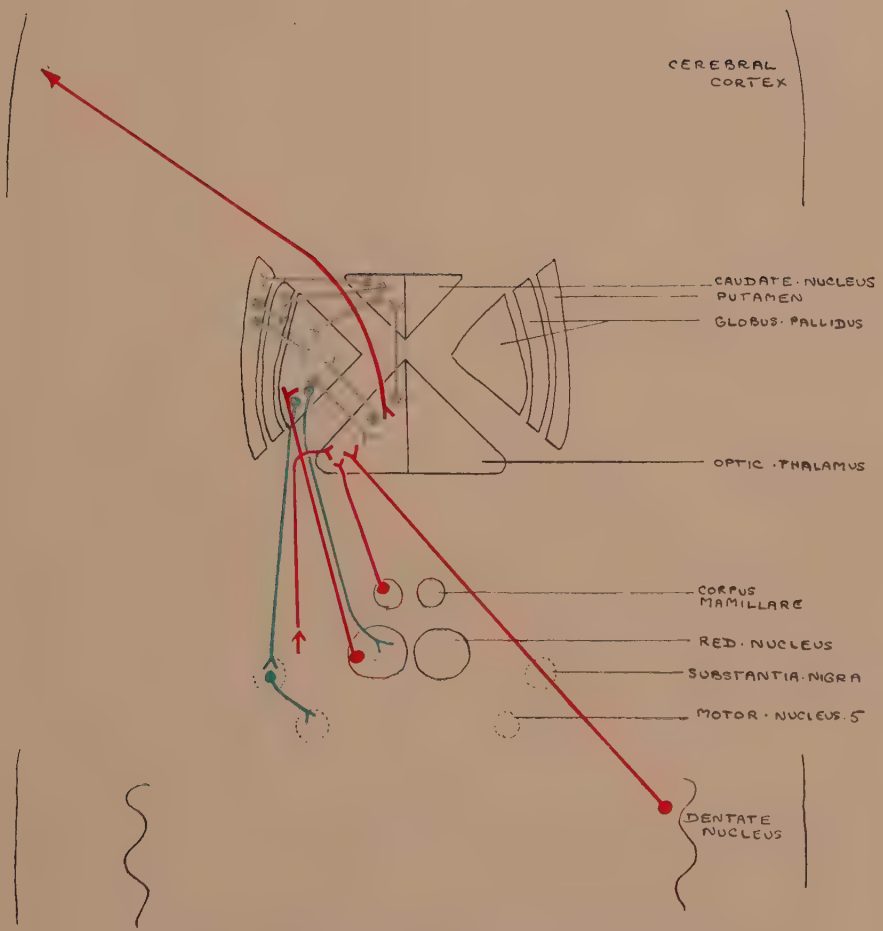

DIAGRAM 31.—Diagram to show Basal Ganglia Connections.

Red : Incoming fibres.
Blue : Interconnecting fibres.
Green : Outgoing fibres.

(iii.) Temporo- and occipito-pontine-cerebellar fibres, from temporal and occipital cortex to nuclei pontis and thence relayed to opposite cerebellar cortex.

(iv.) Last neurone on auditory path passing to temporal cortex, and on visual path passing to occipital cortex.

Thus the anterior part of the anterior limb and the posterior part of the posterior limb contain corticopetal (sensory) fibres, the genu and anterior two-thirds of the posterior limb containing corticofugal (motor) fibres. Between the ascending and descending fibres in both anterior and posterior limbs are found the cortico-pontine-cerebellar fibres. It should be noted that the sensory fibres have a cell station at this level, whereas most of the motor fibres pass through with no connection.

Connections of the Optic Thalamus.

The optic thalamus consists of the following divisions :—

1. Posterior nucleus or pulvinar, with which is intimately associated the external (lateral) geniculate body, receiving and relaying optic impulses.
2. Anterior nucleus, receiving olfactory impulses by fibres from corpus mammillare.
3. Medial nucleus (or essential thalamic organ of Head and Holmes), receiving impulses from the two lateral nuclei and probably concerned with " feeling tone."
4. Lateral nucleus, receiving spinal, trigeminal and medial fillets and relaying all forms of body sensation underlying co-ordinated motion.
   (*a*) Ventral nucleus, receiving ordinary " body sense " impulses.
   (*b*) Dorsal nucleus, receiving fibres from ventral nucleus and determining redistribution of senses.

   Lateral nucleus also gives rise to—
   (*c*) Fibres to the cerebral cortex. (Some of these cross in the corpus callosum to the opposite cortex (Ferrier and Turner).)
   (*d*) Fibres to the caudate and lenticular nuclei.
5. Internal (medial) geniculate body, receiving and relaying auditory impulses from the lateral fillet.
6. Ganglion habenula, which is connected with the hippocampal gyrus and is thus involved in the sensation of smell.

The thalamus is thus a relay station on the path for all sensory impulses.

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CHAPTER VIII

MICROSCOPIC STRUCTURE OF CORTEX OF CEREBELLUM AND OF CEREBRUM

A. Structure of Cerebellar Cortex.

The grey matter of the cerebellar cortex is arranged to form three layers, the middle being incomplete :—

(*a*) *Outer molecular layer*, containing—

1. Dendrites of Purkinje cells.
2. Axons of cells of inner granular layer.

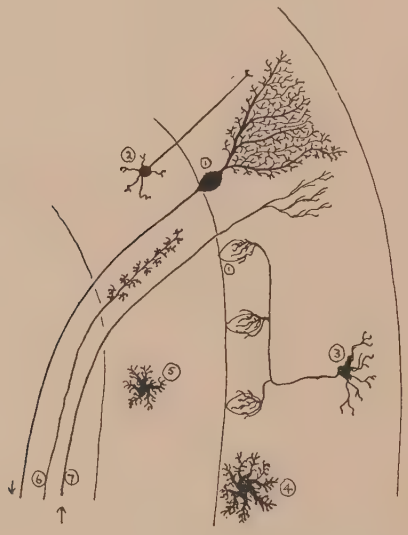

DIAGRAM 32.—Diagram of Cells and Fibres of Cerebellar Cortex.

1. Purkinje Cell.
2. Granule Cell.
3. Basket Cell.
4. Neuroglia Cell.
5. Golgi Cell.
6. Moss Fibre.
7. Tendril Fibre.

(*After Schafer.*)

3. Tendril fibres, or axons of incoming fibres.
4. Star-shaped cells, with axons running parallel to the surface, making a " basket " network round the bodies of the Purkinje cells.
5. Neuroglia cells of various types.

(*b*) *Layer of Purkinje cells*, consisting of large flask-shaped cells, of which

the dendrites arborise in the outer molecular layer, and the axons pass inwards through the inner granular layer to connect with the cerebellar nuclei.

(*c*) *Inner granular (or nuclear) layer*, containing—

1. Axons of Purkinje cells passing through.
2. Granule cells, whose axons run into the molecular layer, and bifurcate at right angles to the plane of arborisation of the Purkinje dendrites.
3. Golgi cells of various types.
4. Moss fibres, or axons of incoming fibres.

Thus the medullary part of the cerebellum contains—

(*a*) Afferent fibres { Moss fibres ending in granule layer. / Tendril fibres ending in molecular layer.

(See Diagram 32.)

(*b*) Efferent fibres, the axons of the Purkinje cells.

B. Structure of Cerebral Cortex.

Many layers have been distinguished in the grey matter of the cerebral cortex by different workers, but the following classification (Bolton) is the most convenient.

The following five layers can be distinguished in all parts of the cortex with the exception of the hippocampus and pyriform lobe, which are archipallium and not neopallium :—

1. Outer fibre lamina (or molecular layer), nerve fibres.
2. Outer cell lamina (or nuclear layer), small pyramidal cells.
3. Middle cell lamina (or granule layer), small nerve cells, usually spherical.
4. Inner fibre lamina (or molecular layer), nerve fibres.
5. Inner cell lamina, polymorphic nerve cells, usually stellate.

Certain variations in these layers occur in different parts of the cerebral cortex, the following being the most important :—

(*a*) *Frontal and parietal areas* (great association areas).

The outer cell layer is very thick, varying directly with the mental capacity of the individual.

(*b*) *Pre-Rolandic area* (motor area).

The inner fibre layer contains the giant pyramidal cells, or Betz cells, whose axons give rise to the pyramidal tracts. The middle cell layer is almost absent.

(*c*) *Post-Rolandic area* (part of sensory area).

The middle cell layer is extremely thick.

(*d*) *Occipital lobe* (visual area).

(i.) Medial aspect (visuosensory cortex).—The middle cell layer is greatly thickened, appearing double, due to an ingrowth of a layer of white fibres, the line of Gennari (outer layer of Baillarger).

(ii.) Outer aspect (visuopsychic cortex).—The outer cell layer is nearly

twice as thick as in the visuosensory area. The line of Gennari ceases at the junction of the two regions.

(*e*) *Temporal lobe* (auditory area).

Variations in structure for auditory sensory and auditory psychic functions are present as in the occipital area for visual functions.

(*f*) *Hippocampal area* (sensory for taste and smell).

Special groups of cells are present in the outer layers. The hippocampus major contains cells whose axons pass out as the alveus, going to form the posterior pillar of the fornix.

The significance of these structural variations will be considered in Part II., Chapter V.

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CHAPTER IX

CEREBROSPINAL FLUID

(A.) Distribution.

The cerebrospinal fluid is found in the lateral ventricles which communicate by the foramina of Monro with the third ventricle ; this in turn communicates by the Sylvian aqueduct with the fourth ventricle and thence to the central canal of the spinal cord. The fluid is thus found in the whole of the cerebrospinal canal. In addition it fills the subarachnoid space, communication being established with the fourth ventricle by the foramen of Magendie (and, according to some, the lateral foramina of Luschka) ; this subarachnoid space is divided into intercommunicating cisternæ.

Every blood vessel perforating into nervous tissue is surrounded by a covering of cells of the arachnoid and pia mater, which turn in with it ; thus it lies in a cell-enclosed channel which communicates directly with the subarachnoid space and is continued to connect with the spaces round the nerve cells, the fluid thus bathing all the neurones.

(B.) Source.

The cerebrospinal fluid is produced by the choroid plexuses, chiefly those in the lateral ventricles, probably by secretion.

Evidence.

(i.) Histological.—Changes can be observed in the cells of the choroid plexus of the type usually associated with secretory activity. Further, the position of the Golgi apparatus in these cells favours the view that they are producing a secretion on their free surface.

(ii.) Direct observation.—The exposed choroid plexus " sweats " on the free surface.

(iii.) Pharmacological.—The flow of fluid from a fistula is increased by ether and pilocarpine and retarded by atropine ; in addition the choroid plexus cells are altered by these drugs.

(iv.) Chemical.—The composition of the fluid is not such as would be produced from blood by physico-chemical means unless the choroid plexus cells exert a marked selective activity.

(v.) Embryological.—Congenital internal hydrocephalus is frequently associated with hypertrophied choroid plexus.

(vi.) Experimental.

(*a*) Internal hydrocephalus follows occlusion of the Sylvian aqueduct.

(*b*) Unilateral internal hydrocephalus follows occlusion of one foramen of Monro, but this is prevented by extirpation of the choroid plexus of that side.

(C.) **Circulation and Absorption.**

The fluid is continuously formed, and consequently it must be continually removed. It passes away by three routes :—

(i.) The Pacchionian bodies of the arachnoid (arachnoid villi), and thence into the venous sinuses, especially the superior longitudinal sinus.

(ii.) The venous plexus round the foramen magnum and thence into the spinal veins.

(iii.) Along the perineural sheath of the nerves, particularly the optic and the auditory nerves.

The method of absorption has been fully investigated by Weed, to whose work reference should be made.

(See Diagram 33.)

(D.) **Pressure.**

The pressure of the cerebrospinal fluid is normally about 4 mm. Hg, equivalent to a flow of one drop per minute when recumbent.

The pressure varies, as a rule, directly as the arterial pressure, but it is possible to vary the blood pressure (*e.g.*, by vagus stimulation) without affecting that of the cerebrospinal fluid. The venous pressure is normally consistently below that of the cerebrospinal fluid, and consequently diffusion occurs into the veins. The reverse can, however, occur : if distilled water is injected intravenously, the occipital headache due to removal of cerebrospinal fluid by puncture is relieved because fluid then diffuses from the veins into the cisterna basalis.

(E.) **Normal Composition.**

Normal cerebrospinal fluid is a clear colourless liquid, of specific gravity 1004 to 1006. The cells usually number less than five per cubic millimetre. The *p*H is between 7·4 and 7·6 (blood = 7·4), but on standing it may rise to 8.

It contains the following :—

Glucose : varying from 0·05 to 0·08 gm. per 100 c.c.

Protein : trace, about 0·02 gm. per 100 c.c.

Inorganic salts, as in blood plasma.

(Chlorides = 0·73 to 0·75 gm. NaCl per 100 c.c.)

Urea : slightly less than in plasma.

Active principles from pituitary gland.

CO_2, in excess of that in the blood.

It contains no antibodies and no opsonins, and does not clot on standing.

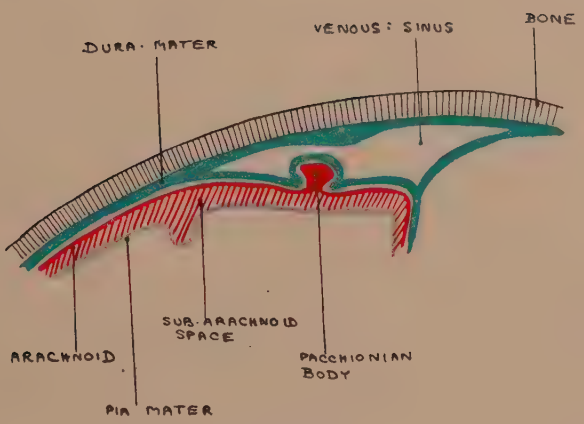
DURA · MATER
VENOUS : SINUS
BONE
SUB · ARACHNOID SPACE
ARACHNOID
PACCHIONIAN BODY
PIA MATER

DIAGRAM 33.

(F.) **Functions.**

The more important functions of the cerebrospinal fluid are as follows :—

(i.) Acts as a mechanical support for nervous tissues, being protective by equalising the pressure within and without, and by providing a pressure independent of the arterial blood pressure.

(ii.) Helps to regulate the blood supply to the brain. The extent to which this occurs is somewhat doubtful ; Macleod regards the volume of fluid as too small to exert much effect, whereas other writers (Weed) believe that it plays a large part.

(iii.) Acts as intermediary for O_2, nutriment, CO_2, and waste, between the blood and nervous tissues, as it bathes all the neurones.

(iv.) Is protective to nervous tissues in that the choroid plexus does not allow of the passage of blood poisons into the cerebrospinal fluid.

(G.) **Variations in Composition.**

(i.) *Physical Changes.*

The fluid may be turbid (as in septic meningitis) or bloodstained. It may be clear, but clot on standing (as in tubercular meningitis). It is sometimes straw-coloured.

(ii.) *Cell Content.*

The number of cells is increased in inflammation.

Lymphocytes are increased in all acute infections, especially tubercular meningitis, encephalitis lethargica, anterior poliomyelitis, and all syphilitic affections of the nervous system.

Polymorphonuclear leucocytes are increased in all pyogenic infections.

Large mononuclear cells appear in all cases of tumours involving the meninges.

(iii.) *Glucose Content.*

As determined by Fehling's method, this is increased in diabetes and decreased in septic meningitis, and usually decreased in tubercular meningitis and in any other meningitic affections.

(iv.) *Protein Content.*

Globulin increase is a definite indication of breakdown of nerve cell tissue, and of increased permeability of inflamed blood vessels. Consequently its amount is constantly increased in diseases such as tabes, meningo-myelitis, and general paralysis of the insane.

Lange's colloidal gold test depends on the fact that the $\frac{\text{globulin}}{\text{albumin}}$ ratio is increased in central nervous syphilis. The precipitation is due to the globulin ; in normal cerebrospinal fluid there is sufficient albumin to prevent this precipitation from occurring. The curve so obtained by the colour reactions is a very reliable diagnostic factor in distinguishing between tabes, meningitis, and general paralysis of the insane.

(v.) *Chloride Content.*

This is reduced in tubercular meningitis.

(vi.) *Abnormal Constituents.*

In conditions of excessive breakdown of nervous tissue cholesterol and choline are present.

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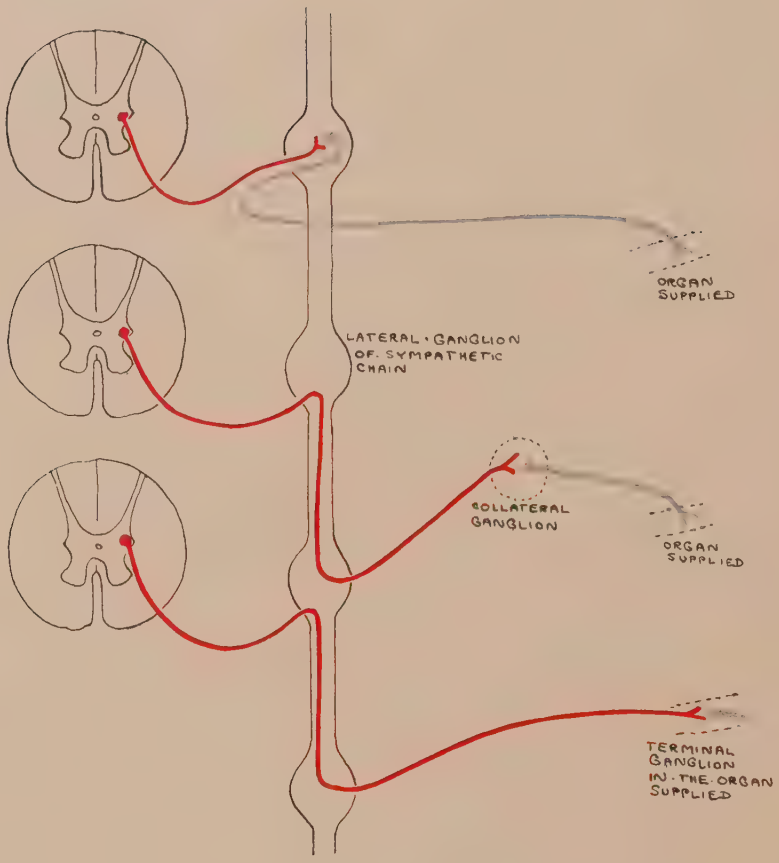

DIAGRAM 34.—Diagram to show Ganglion Connections of the Autonomic System.

Red : Pre-ganglionic fibre. Blue : Post-ganglionic fibre.

CHAPTER X

AUTONOMIC NERVOUS SYSTEM

THE autonomic nervous system is sometimes defined as that part of the nervous system which is independent of the control of the will. This definition is not strictly correct, as certain reflexes carried out by the central nervous system (*e.g.*, knee jerk) cannot be voluntarily prevented. Langley describes the autonomic nervous system as consisting " of the nerve cells and nerve fibres by means of which efferent impulses pass to tissues other than multinuclear striated muscle " (*i.e.*, chiefly glands and smooth muscle). It is, however, usual to include also certain afferent fibres that pass from the viscera and that carry impulses producing reflex responses by the efferent autonomic fibres.

There is one important anatomical difference between this and the central nervous system. The efferent path of the autonomic nervous system always consists of two neurones, the first belonging to the central nervous system, the axon emerging in one of the cranial or spinal nerves and ending round the dendrites of a sympathetic cell in some ganglion, and the second consisting of the cell in the sympathetic ganglion whose axon passes to the peripheral tissue. The fibres emerging from the central nervous system are known as pre-ganglionic, and are medullated ; these constitute the white rami communicantes. The post-ganglionic fibres passing from the ganglion to the organ as the effector nerves are usually non-medullated ; these are the grey rami communicantes (see Diagram 34).

The efferent autonomic nervous system thus consists of the pre-ganglionic and post-ganglionic fibres. The pre-ganglionic fibres represent the connector fibres of a simple reflex arc (see Part II., Chapter VIII.), and arise in connector cells, the fibres passing out from the brain and cord in connection with certain nerves and ending in ganglia in various positions. The afferent part of the arc varies, and may come straight from the viscera by posterior root fibres (see "Afferent Autonomic System " below), or through higher centres, *e.g.*, in the medulla.

These pre-ganglionic fibres are given off from three distinct regions of the central nervous system. The terminology applied to these groups is somewhat confusing, but the following is adopted as being the most reasonable :—

A. *True sympathetic*, or thoracico-lumbar outflow.

Fibres emerge from the spinal cord between the first thoracic and third lumbar segments (possibly also L. 4).

B. *Parasympathetic*, or cranio-sacral outflow.

Fibres emerge—

(i.) In cranial nerves 3, 7, 9, 10, and 11 (cranial outflow).

(ii.) In sacral nerves 2, 3 (sacral outflow).

This division into sympathetic and parasympathetic fibres is not an arbitrary

one, but depends both on anatomical arrangement and on physiological characteristics.

Position of the Autonomic Ganglia.

We owe our knowledge of the position of the cell stations of the autonomic paths to Langley, who devised the nicotine method for tracing fibres. Nicotine paralyses the connection between pre-ganglionic fibre and nerve cell, but does not affect the actual nerve fibres. If, therefore, an appropriate ganglion is painted with nicotine, stimulation of the preganglionic fibres will produce no response, whereas stimulation of the post-ganglionic fibres will do so. By this means it is possible to pick out the ganglion in which definite fibres have their cell station.

The autonomic ganglia fall into three groups :—

(i.) *Lateral ganglia*, or sympathetic chain, consisting of paired chains of ganglia extending through the thoracic and lumbar region, and forward into the cervical region. The ganglia corresponding to the cervical and upper thoracic segments are fused into the superior and inferior cervical and stellate ganglia, the paired chains corresponding to every segment from T. 4 to S. 3.

(ii.) *Collateral or intermediate ganglia*, including the ciliary, otic, submaxillary, semilunar, superior and inferior mesenteric ganglia.

(iii.) *Distal or terminal ganglia*, including groups of ganglion cells in the walls of the organs supplied, *e.g.*, in the heart and intestine.

The sympathetic pre-ganglionic fibres have cell stations in either the lateral or collateral ganglia, whereas the parasympathetic pre-ganglionic fibres usually terminate in the distal ganglia. The importance of this arrangement lies in the synapse, because one pre-ganglionic fibre connects with many cells and thus influences many post-ganglionic fibres, the ganglia functioning as distributing stations. Thus the visceral nerves can produce rapid, widespread, diffuse and generalised effects, whereas the somatic nerves arising from anterior horn cells and with no extra-central station are for accurate localised responses.

Before considering the nerves in greater detail a short summary giving the cell station and distribution of the more important fibres may help to give a clearer picture of the plan on which this system is built up. (See p. 41.)

A. Thoracico-lumbar or True Sympathetic Fibres.

White rami from the lateral horn cells of segments T. 1 to L. 2 pass out to the sympathetic chain of ganglia, running either up or down, some connecting with these ganglia and others passing through the chain and running out to make connections with outlying ganglia.

These fibres provide secretory impulses to the sweat glands, vasoconstrictor impulses to the arterioles, motor fibres to the erector pili muscles, inhibitory fibres to the muscles of the bronchioles, œsophagus, stomach, intestine and bladder, motor fibres to the cardiac, ileocolic and anal sphincters, accelerator fibres to the heart, both motor and inhibitor fibres to the uterus, ureters, Fallopian tube and vas deferens.

	Origin.	Nerves carrying the Fibres.	Cell Station.	Distribution.
Cranial parasympathetic.	Mid-brain.	Cr. 3.	Ciliary ganglion.	Intrinsic eye muscles.
	Medulla.	Cr. 7, 9.	Meckel's, otic, submaxillary, sublingual ganglia.	Vessels and glands of nose and mouth.
		Cr. 10, 11.	Mostly in the organs.	Alimentary canal, heart, bronchi, pancreas.
Sympathetic.	Thoracico-lumbar cord.	Sp. T. 1 to L. 3 or 4.	Lateral ganglia.	Sweat glands, hairs, and blood vessels of body-wall and skin.
			Collateral ganglia—*e.g.*, mesenteric.	Abdominal organs.
Sacral parasympathetic.	Sacral cord.	Sp. S. 2, 3.	Mostly terminal.	External genitalia, bladder, and lower part of alimentary canal.

Splanchnic Nerves.

These nerves belong to the true sympathetic system, and are made up as follows :—

(i.) *Great Splanchnic.*

Arises from the sympathetic chain between T. 5 and T. 10 ; the emerging fibres join to make the great splanchnic nerve. Opposite T. 11 or T. 12 the splanchnic ganglion is formed upon this nerve, and from this arise branches for the supply of the œsophagus. The nerve then passes to the anterior end of the cœliac ganglion.

(ii.) *Small Splanchnic.*

Arises from the sympathetic chain opposite T. 9 and T. 10, and ends in the cœliac plexus.

(iii.) *Least Splanchnic.*

Arises from the sympathetic chain opposite T. 12, and ends in the renal plexus.

Cervical Sympathetic.

This contains fibres, chiefly from T. 1, 2, 3, that have passed up through the annulus of Vieussens and the inferior cervical ganglion, and end in the superior cervical ganglion. From here the post-ganglionic fibres—

(i.) Pass through the ciliary ganglion by the short ciliary nerves to supply

the dilator pupillæ muscle, the unstriped muscle in the levator palpebræ superioris which retract the upper eyelid, and the unstriped muscle (Muller's) at the back of the eye;

(ii.) Pass by the four upper cervical nerves to supply the skin (in the cutaneous sensory branch) and the buccal glands, salivary and lachrymal glands, *viâ* the plexuses along the corresponding blood vessels.

A few of the cervical sympathetic fibres end in the middle cervical ganglion, and thence the post-ganglionic fibres supply the thyroid.

B. **Sacral Autonomic (Parasympathetic) Fibres.**

The white rami from cells of the lateral part of the grey matter of the cord at the level S. 2 and 3 pass out, and unite as the pelvic nerves or nervi erigentes. These pass to the bladder, part of the large intestine, blood vessels of the penis, and muscle fibres round the prostate and of the clitoris, the cell stations being in the organs supplied.

C. **Cranial Autonomic (Parasympathetic) Fibres.**

These fibres emerge in the cranial nerves 3, 7, 9, 10, and 11.

(i.) *Third Nerve.*—Cells of origin—anterior end of nucleus 3.

Pre-ganglionic fibres pass to ciliary ganglion.

Post-ganglionic (non-medullated) fibres pass in short ciliary nerves to ciliary muscle and sphincter pupillæ.

(ii.) *Seventh Nerve.*—Cells of origin—motor nucleus of 7.

Pre-ganglionic fibres pass in pars intermedia to join main part of facial passing *through* geniculate ganglion. They then pass by—

Either (*x*), great superficial petrosal nerve, to Meckel's ganglion; from here the post-ganglionic fibres pass by (*a*) temporomalar nerve to lachrymal gland and (*b*) palatine nerves to palate and naso-pharynx:

Or (*y*), chorda tympani, to join lingual nerve, and thence to ganglia in connection with salivary glands, the post-ganglionic fibres supplying these glands.

(See Diagram 29.)

(iii.) *Ninth Nerve.*—Cells of origin—main (dorsal) nucleus of 9.

Pre-ganglionic fibres pass in tympanic nerve through tympanic plexus and by lesser superficial petrosal nerve to otic ganglion.

Post-ganglionic fibres, by auriculo-temporal nerve to parotid gland.

(iv.) *Tenth Nerve.*—Cells of origin—main (dorsal) nucleus of 10 (nucleus intercalatus).

Pre-ganglionic fibres pass in vagus, ending in cells lying in the organs supplied (see below).

(v.) *Eleventh Nerve.*—Accessory part, actually part of 10 (see Part I., Chapter VI.).

Autonomic Supply of Certain Special Structures.

Many structures have both a sympathetic and a parasympathetic supply; some of the more important are summarised below, the function assigned being in all cases carried out by the post-ganglionic fibres.

1. Alimentary Canal (other than rectum).

In general the vagus increases the tone of the muscle, and promotes peristalsis; it is also secretomotor to the glands. It also carries the afferent impulses.

(*a*) *Œsophagus.*

(i.) Sympathetic. T. 5–10. Fibres run as splanchnic nerve, with cell station in splanchnic ganglion.
Inhibitor to muscle wall. Motor to cardiac sphincter.

(ii.) Parasympathetic. Vagus, with cell station in muscle wall.
Motor to muscle wall. Inhibitor to cardiac sphincter.

(*b*) *Stomach.*

(i.) Sympathetic. T. 5–10. Fibres run as splanchnic nerve with cell station in cœliac ganglion (solar plexus).
Inhibitor to muscle wall.
Motor to pyloric sphincter.

(ii.) Parasympathetic. Vagus, with cell station in muscle wall.
Motor to muscle wall.
Inhibitor to pyloric sphincter.

Both groups mingle in Auerbach's and Meissner's plexuses.

(*c*) *Small Intestine.*

(i.) Sympathetic. T. 5–10. Fibres run as splanchnic nerve with cell station in superior mesenteric ganglion.
Inhibitor to muscle wall.
Motor to ileocolic sphincter. (Tone of sphincter is due to sympathetic supply.)

(ii.) Parasympathetic. Vagus, with cell station in muscle wall.
Motor to muscle wall. (Stimulation has no effect on sphincter.)
Motor to gall-bladder.

2. Rectum, Anal Canal and Anus.

(i.) Sympathetic. L. 1–4. Fibres run with cell station in inferior mesenteric ganglion.
Inhibitor to gut wall.
Motor to anal sphincter.

(ii.) Parasympathetic. S. 2, 3. Fibres run as nervi erigentes, with cell station in gut wall.
Motor to gut wall.
Inhibitor to anal sphincter.

(iii.) Afferent fibres chiefly in nervi erigentes.

3. Bladder.

(i.) Sympathetic. L. 1–4. Cell station in inferior mesenteric ganglion ; post-ganglionic fibres pass in hypogastric nerves.
Inhibitor to bladder wall.
Motor (constrictor) to sphincter.

(ii.) Parasympathetic. S. 2, 3. Fibres run as nervi erigentes, with cell station in bladder wall (hypogastric plexus).
Motor to bladder wall.
Inhibitor to sphincter.

(iii.) Spinal. S. 1, 2. Pass as pudic nerve.
Motor to compressor urethræ muscle.

(iv.) Afferent fibres chiefly in nervi erigentes.

4. Uterus, Fallopian Tube, Vas Deferens, and Ureter.

(i.) Sympathetic. Cell station in or near organs supplied.
Both motor and inhibitor to muscle.

(ii.) Parasympathetic. No supply.

5. Heart.

(i.) Sympathetic. T. 1–3. Fibres have cell station in stellate ganglion. Post-ganglionic fibres travel in cardiac branches from inferior and superior cervical ganglia to heart.
Motor (accelerator).

(ii.) Parasympathetic. Vagus. Cell station in region of sino-auricular or auriculo-ventricular nodes.
Inhibitor.

6. Bronchioles.

(i.) Sympathetic. Post-ganglionic fibres from stellate ganglion.
Inhibitor (relaxing).

(ii.) Parasympathetic. Vagus.
Motor (contracting).

(See Diagram 35.)

7. Limbs.

The vasomotor and sweat fibres to the limbs (sympathetic) arise from the spinal cord as white rami and pass into the sympathetic chain. The post-ganglionic fibres then pass back as grey rami to join certain of the spinal nerves that make up the great limb plexuses.

(See Diagram 36.)

Afferent Part of the Autonomic System

Afferent fibres from the viscera carrying afferent impulses from these structures and belonging to the autonomic system pass into the brain and cord by posterior root fibres at levels corresponding to the outflow of the autonomic fibres. The healthy viscera are insensitive to the usual stimuli

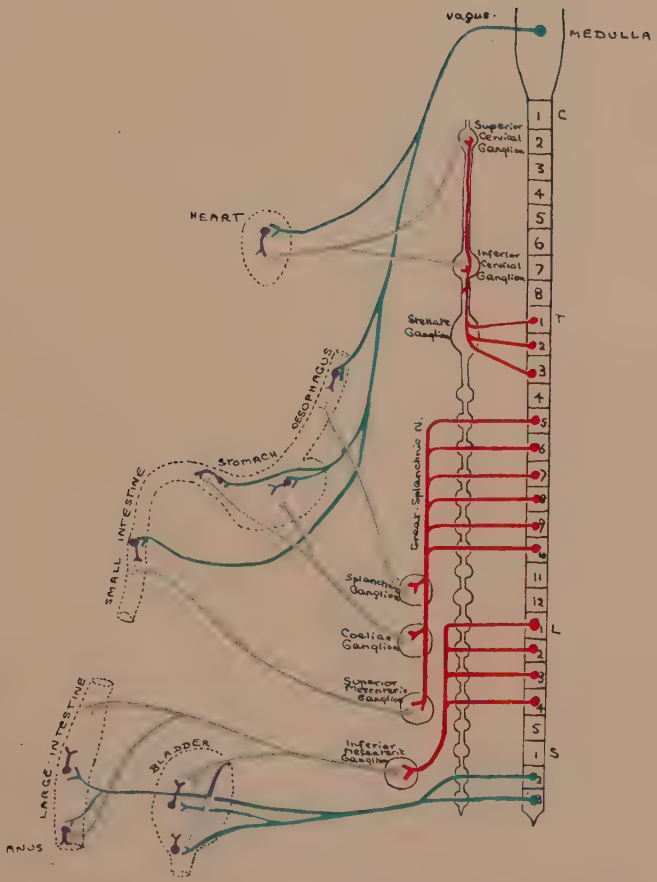

DIAGRAM 35.—Diagram of Autonomic Supply of Certain Organs.

Sympathetic :—
Red : Pre-ganglionic.
Blue : Post-ganglionic.

Parasympathetic :—
Green : Pre-ganglionic.
Mauve : Post-ganglionic

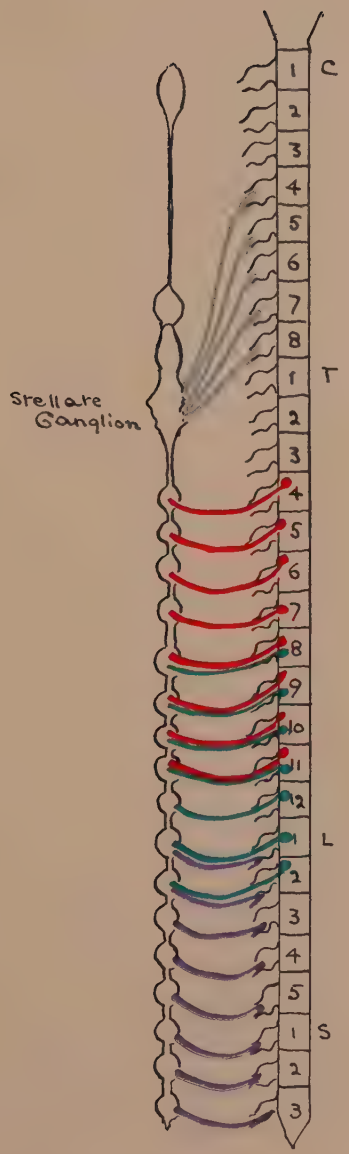

DIAGRAM 36.—Diagram to show Nerve Distribution of Vasomotor Fibres to the Limbs.

Arm.—Pre-ganglionic, T4–T11. Post-ganglionic, C4–C8.
Leg.—Pre-ganglionic, T8–L2. Post-ganglionic, L1–S3.

which produce sensation in the outer body wall, such as pain and temperature stimuli, but violent pressure changes occurring in a hollow viscus produce a sensation of pain ; this sensation is referred not to the viscus affected, but to a definite area on the surface of the body. This phenomenon is known as " referred pain," and is explained by the fact that the afferent nerves from the viscera (splanchnic afferents) terminate in the cord in close association with the afferent nerves from certain skin areas (somatic afferents) ; thus the sensation from the viscus is referred to the peripheral distribution of the cutaneous fibres, which is of a definitely segmental arrangement.

By investigating the cutaneous areas of " referred pain " due to impulses from the viscera it is possible to determine the probable course of the afferent autonomic fibres from these organs. The following distribution is usually accepted :—

Organ.	Spinal nerves whose cutaneous distribution corresponds with the area of " referred pain."
Heart	T. 1–3.
Lungs	T. 1–5.
Stomach	T. 6–9.
Intestine	T. 9–12.
Rectum	S. 2–4.
Liver and gall bladder	T. 7–10.
Kidney and ureter	T. 10–12, L. 1.
Bladder	T. 12, L. 1–2.
Prostate	T. 10, 11.
Testis and ovary	T. 10.
Uterus	T. 10–12, L. 1.

The afferent impulses from the viscera normally produce reflex responses in regulating the activity of various " involuntary " structures, such as unstriped muscle and glands ; these effects are known as " visceral reflexes." The more important of these reflexes are associated with the heart, the respiratory system, and the alimentary system.

(*a*) *Cardiac Reflexes.*—Afferent impulses pass from the heart to the medulla and reflexly affect the rate of beat. From the arch of the aorta impulses passing up in the depressor fibres inhibit the vasomotor centre (causing fall of blood pressure) and stimulate the vagus centre (slowing the beat). From the great veins and right auricle impulses pass up the vagus and depress the vagus centre and stimulate the sympathetic accelerator fibres. Impulses from other viscera can also reflexly affect the heart, as, for example, from the stomach.

(*b*) *Respiratory Reflexes.*—Afferent impulses pass from the lungs in the vagus to the respiratory centre, regulating its rate of activity. Other reflex respiratory effects are produced by irritation of the nerve endings in the lungs or the pleura.

(*c*) *Local Reflexes in Abdominal Viscera.*—It is probable that a large degree of correlation is effected between the abdominal viscera by local nerve reflexes, which are of the nature of the visceral reflexes.

(*d*) *Visceral Reflexes in Disease.*—Under abnormal conditions the afferent visceral impulses may also provoke motor responses in structures other than "involuntary." For example, in angina pectoris the afferent impulses from the heart may cause excessive salivary secretion, a viscero-secretory reflex, and in certain visceral diseases the visceral afferent impulses may produce viscero-motor reflexes, as evidenced by strong and lasting contraction of certain muscles.

Functions of the Autonomic System

The functions of this system are perhaps best understood by considering the results of stimulation of the true sympathetics and of the parasympathetics.

(*a*) *Sympathetic Stimulation.*

Stimulation of the sympathetic system produces widespread results, all of which serve to activate the body for a struggle and to increase its powers of defence. A few examples will make this clear :—

(i.) The pupil dilates—*i.e.*, there is an increased perception of light.

(ii.) The heart beats more quickly and forcibly—*i.e.*, there is an increased blood supply to the muscles.

(iii.) There is vasoconstriction in the splanchnic area—*i.e.*, there is a rise of blood pressure, and blood is driven from the digestive area to the skeletal and cardiac muscles, lungs and brain.

(iv.) There is stimulation of the sweat glands—*i.e.*, the body is cooled, so getting rid of the heat produced by muscular effort.

(v.) The hairs are erected—*i.e.*, the animal assumes a more alarming appearance.

These effects are all of the katabolic type, produced by or causing a utilisation of energy and breakdown of material.

(*b*) *Parasympathetic Stimulation.*

The effects produced by parasympathetic stimulation are comparatively localised, because the cell stations are close to the ultimate destination. The nerves belonging to the cranial outflow produce effects that lead to fortifying against a sudden need or time of strain and a building up of the necessary body reserves, whereas the sacral outflow is of "internal service to the body in the performance of acts leading immediately to greater comfort" (Cannon). A few examples will again make this clear :—

(i.) The pupil contracts—*i.e.*, the retina is shielded.

(ii.) The heart-beat is slowed—*i.e.*, there is a longer rest period for the muscle.

(iii.) The flow of saliva and gastric juice is increased, and the tone of the alimentary muscle is raised—*i.e.*, conditions are produced that favour digestion of food and its absorption.

(iv.) The bladder and rectum are emptied—*i.e.*, waste material is removed from the body.

These effects are mostly of the anabolic type, producing a conservation or building up of material.

Gaskell has shown that where sympathetic and parasympathetic fibres are distributed to the same structure the effects of stimulation of the nerves are antagonistic.

	Sympathetic stimulation.	Parasympathetic stimulation.
Pupil	Dilated.	Constricted.
Heart	Accelerated.	Slowed.
Peristalsis of intestine . . .	Inhibited.	Increased.
Bladder sphincter . . .	Constricted.	Relaxed.

Thus in pain, fear, rage and excitement the sympathetic neurones are rapidly stimulated, the effects being increased by consequent and accompanying outpouring of adrenin; simultaneously the parasympathetics are inhibited so that the defensive katabolic activities can be carried on.

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PART II

CHAPTER I

THE NORMAL PHYSIOLOGY OF THE SENSORY PATH

THE sensory path is frequently taken as synonymous with the ascending path, although the " sensory " impulses are, strictly speaking, only those which reach consciousness and evoke a sensation ; it is, therefore, more correct to speak of the afferent or ascending impulses if the term is to include those which reach higher centres other than the cortex of the cerebrum.

The sensory path is an extremely complex one, but nearly all the fibres relay through the optic thalamus ; one would, therefore, expect to find that this region plays an important part in the interpretation of the afferent impulses. The type of sensation evoked depends always on the type of end organ stimulated, and this explains why stimulation of the sensory cerebral cortex does not produce a sensation that is related to the stimulus. The special sensations of sight, hearing, smell and taste will be considered separately ; the following description applies to general or ordinary sensation only.

Ordinary sensation is usually grouped into two divisions : deep sensibility and superficial or cutaneous sensibility.

(*a*) *Deep Sensibility.*—This includes afferent impulses coming from the deep structures, such as muscles, joints, and tendons. The sensations produced are those of " muscle sense," stereognosis, vibratory sense, and a sense of pressure-pain. The fibres conveying these afferent impulses pass in the so-called motor nerves of the muscles.

(*b*) *Cutaneous Sensibility.*—This includes afferent impulses coming from the skin, the fibres passing in the cutaneous branches of the nerves. Cutaneous sensibility is of two kinds : protopathic and epicritic.

Protopathic Sensibility.—This is a somewhat crude and primitive type of sensation, that is not localised to the spot stimulated, but is of a radiating nature. It includes—

(i.) Recognition of gross differences of temperature, *i.e.*, a sensation of cold below 25° C., and of heat above 38° C., but no sensation of " temperature " between 25° C. and 38° C.

(ii.) Recognition of pain, but with a high threshold and excessive reaction, and no localisation.

Epicritic Sensibility.—This is a more highly differentiated type of sensation that is accurately localised to the spot stimulated. It includes—

(i.) Recognition of light touch (tactile sensation).

(ii.) Recognition of variations in temperature, including those between 25° C. and 38° C.

(iii.) Recognition of pain, with a low threshold and normal reaction, the sensation being accurately localised.

(iv.) Recognition of simultaneous stimulation of two points—tactile discrimination.

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This classification of the types of sensation depends on the experiments originally carried out by Head and Rivers, and later confirmed by other workers. Division of a cutaneous nerve is followed by complete loss of epicritic sensation in the area supplied by the nerve cut, and loss of protopathic sensation over a somewhat smaller area within this ; deep sensation is not interfered with. This difference in the areas affected is due to overlapping of the distribution of nerves carrying protopathic sensation, and to the accurately segmental distribution of those carrying epicritic sensation. As regeneration of the nerve occurs protopathic sensation returns first and is complete in about thirty weeks. Some workers consider that fibres carrying protopathic sensation are non-medullated, and therefore regenerate very rapidly. Epicritic sensation returns much more slowly, but not always completely, there being no further improvement in function after the lapse of two years.

THE PATH OF THE SENSORY IMPULSES

A. Receptors.

The receptors are the specialised nerve endings that respond to the various sensory stimuli, but the particular receptor subserving a particular sensation is not definitely known. The chief sensory nerve endings are the following :—

(i.) Deep.
- (*a*) Muscle spindles in striped muscle.
- (*b*) Organs of Golgi in tendon.

(ii.) Superficial.
- (*a*) Pacinian corpuscles.
- (*b*) Tactile corpuscles.
- (*c*) End bulbs.
- (*d*) Free terminal branchings.

The cutaneous sensations are not distributed evenly over the whole skin, but in discrete spots, corresponding, no doubt, to the distribution of the specialised nerve endings. This can be demonstrated by mapping out in a certain area those spots of which stimulation of various kinds gives rise to the different kinds of sensation.

B. Path in the Spinal Cord.

All the impulses enter by the posterior root fibres.

(See Diagram 37.)

(i.) *Columns of Goll and Burdach.*

The column of Goll carries impulses from the lower limbs and lower half of the trunk, and that of Burdach from the upper limbs and upper half of the trunk, the column of Goll being pushed medially by the fibres of Burdach. The fibres pass straight up to the nucleus gracilis (Goll) and the nucleus cuneatus (Burdach). The next neurone passes by—

(*a*) External arcuate fibres to the cerebellum or

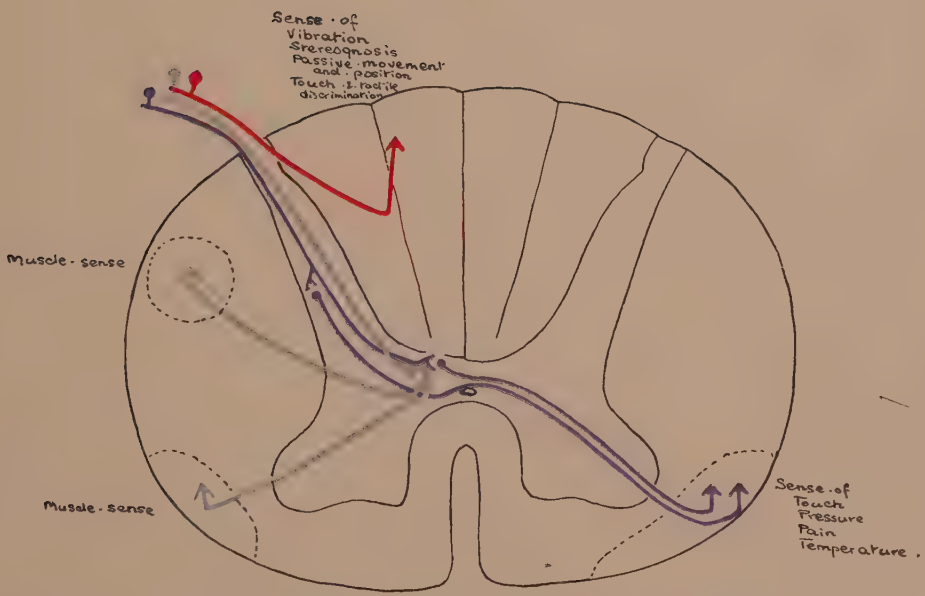

DIAGRAM 37.—Diagram of Paths of Various Sensory Impulses.

(*b*) Internal arcuate fibres (sensory decussation) and medial fillet to the optic thalamus.

The third neurone passes to the post-Rolandic cerebral cortex. (Some workers postulate an extra connecting neurone in the thalamus.)

The sensations carried are—

(*a*) Vibration.

(*b*) Stereognosis.

(*c*) Sense of passive movement and sense of position, including muscle sense.

(*d*) Some touch and tactile discrimination.

(ii.) *Direct and Indirect Cerebellar Tracts.*

The entering fibres arborise round Clarke's cells of the same side. The next neurone carries the impulses by—

(*a*) The direct cerebellar tract to the cerebellar cortex of the same side by the inferior peduncle,

(*b*) The indirect cerebellar tract to the cerebellar cortex of the same side by the superior peduncle.

The sensations carried are those from the muscles, joints, and tendons (*i.e.*, muscle sense). This is sometimes called " unconscious muscle sense," as impulses reaching the cerebellum and producing " reflex " movements do not arouse consciousness.

(iii.) *Spinotectal and Spinothalamic Tracts.*

The entering fibres arborise round Clarke's cells and posterior horn cells of the same side. The next neurone fibres cross in the posterior commissure (some run up for several segments before crossing) and then pass up in the antero-lateral ascending tract, the spinotectal to the inferior corpora quadrigemina and the spinothalamic to the optic thalamus.

(American writers divide these two tracts into ventral and dorsal spinothalamic, taking all the impulses to the thalamus. The ventral spinothalamic would appear to correspond to the spinotectal.)

The next neurone carries the impulses to the post-Rolandic cerebral cortex.

The sensations carried are those of touch, pressure, pain, and temperature, all impulses of one kind, both protopathic and epicritic, passing up together in the spinal cord. Low down in the cord the crossing of all fibres is nearly transverse, but as the cord is ascended the fibres cross more obliquely. Fibres carrying sensations of pain cross most transversely, and those of touch most obliquely. Sensations of pain, heat and cold travel by the spinothalamic tract (dorsal spinothalamic), and those of touch and pressure by the spinotectal tract (ventral spinothalamic).

C. Part played by the Optic Thalamus and Cortex Cerebri respectively.

Almost all the sensory impulses are relayed in the optic thalamus, and this nucleus plays an important part in the appreciation of these impulses. The last neurone on the sensory path carries the impulse to the sensory cortex, *i.e.*, general

sensation to the post-Rolandic area, sensation of sight to the occipital region, of hearing to the temporal region, and of smell to the olfactory lobe. In these areas of the cortex are stored the memories of previous afferent impulses of similar nature, and by interaction with these the cortex is able to interpret and appreciate the precise nature of the stimulus and to localise its origin. But the thalamus also responds to all these stimuli that can provoke a sensation, although in a more crude way.

Our knowledge of the part played by the thalamus is due largely to the work of Head. All sensory impulses possess a " feeling tone " component that gives rise to an emotional response ; in other words, all impulses give rise in a certain degree to a painful or pleasurable impression. The painful or pleasurable component of the impulse is spoken of as " feeling tone," and it is this that is appreciated by the thalamus. Normally an impulse arousing thalamic activity passes on to the cerebral cortex, and this " modifies the crude sensation of the thalamus by giving it a discriminating and intellectual stamp," the thalamic response being controlled by the corticothalamic fibres.

This distinction is perhaps best seen under conditions where there is interference with the corticothalamic path. The thalamus, released from cortical control, then overacts to the feeling tone stimulus. If a patient in this condition is stimulated by a pin-prick on the finger, he will say, " Something is happening to me ; I am being hurt," whereas a normal individual would say, " You are sticking a pin into my finger." There is no localisation of the stimulus and no discrimination as to the type of stimulus, but an over-reaction to its painful component. Similarly, if a glass of hot water is placed in the patient's hand, he will merely recognise the contact of the object and will know that it is unpleasantly hot ; he will not realise the shape, size or texture of the vessel, nor will he know what part of his hand is holding it, nor will he appreciate how hot it is.

The uncontrolled thalamic response thus gives rise to crude sensation with no discrimination. There is also a high threshold value for the stimulus, a long latent period, and a persistence of the sensation after removal of the stimulus. The characteristics of the cortical response are that there is discrimination of the stimulus brought about by comparison, by similarity and difference, with memories of previous impulses reaching the same part of the cortex, and in addition there is spatial perception in three directions, or stereognostic sense. An afferent stimulus capable of provoking a sensation will thus receive full interpretation of all its components because it will arouse the activity of both the thalamus and the appropriate sensory area of the cortex cerebri ; but the kind of sensation produced depends entirely upon the nerve ending stimulated.

The type of sensation known as " referred pain " has already been considered (Part I., Chapter X.).

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CHAPTER II

RESULTS OF INTERFERENCE WITH THE GENERAL SENSORY PATH AT VARIOUS LEVELS

THIS chapter should be read in conjunction with Chapter I. of Part II., which deals with the normal physiology of the sensory path. Interference with this path includes—

1. Irritation.
2. Partial destruction involving delay in conduction.
3. Complete destruction.

The resulting lesions will therefore vary in each case.

An *irritative* lesion always produces intense pain, which may be referred to the distribution of a single nerve, as, for example, in sciatic neuralgia.

Partial destruction produces altered conduction, so that there is delay, and a stronger stimulus is required to produce a characteristic reaction. There is also a sensation of tingling, numbness or pricking in the affected area, and this is often interpreted as hyperæsthesia.

Complete destruction of a conducting path leads to the complete loss of all forms of sensation normally passing along that route.

The results of destructive lesions at different levels in the sensory path will now be considered, beginning at the periphery and working upwards.

1. Peripheral Receptors.

Destruction, either primary or secondary, of nerve endings produces anæsthesia of the part involved.

2. Cutaneous Nerves.

Section of a cutaneous nerve causes anæsthesia of the area innervated.

Loss of epicritic sensation corresponds exactly to the distribution of the nerve. Loss of protopathic sensation is over a smaller area, because of the overlapping of nerves carrying this sensation.

3. Posterior Root Fibres.

Section of these fibres leads to—

(*a*) Anæsthesia due to division of the primary afferent fibres coming from the skin, etc.

(*b*) A lack of muscular control (ataxia), due to section of the secondary afferent fibres from muscles which "correct" the degree of muscular response.

(*c*) Loss of muscle tone and disuse atrophy of the muscles innervated. There is no reaction of degeneration.

(*d*) Loss of reflexes of the level involved.

(*e*) Trophic lesions of the skin in the area innervated.

(*f*) Degeneration of the columns of Goll, Burdach and Lissauer, and of the comma tract, for a short distance, and a consequent interference with the tendon reflexes.

(See Part II., Chapter VIII.)

If the lesion involves irritation, there will also be " lightning pains " (characteristic of tabes), and often " herpes zoster " and neuralgic pain.

4. **Conducting Paths in the Cord.**

(*a*) *Goll and Burdach.*

(These are destroyed, for example, in tabes dorsalis and in postero-lateral sclerosis of the spinal cord.)

Interference with these columns produces—

(i.) Loss of stereognosis and interference with the sense of position.

(ii.) Interference with the tendon reflexes.

(iii.) Loss of vibration sense.

(iv.) Some loss of touch.

In tabes the spinal ganglia are also involved; consequently the effects will include those mentioned under 3 and 4 (*a*).

(*b*) *Cerebellar Tracts.*

Such interference affects the cerebellar maintenance of posture and so leads to ataxy.

(*c*) *Spinothalamic and Spinotectal Tracts.*

Complete destruction leads to the loss of all ordinary sensation except that which travels in the columns of Goll and Burdach.

Partial destruction produces a discrimination between the different types of sensation (such as occurs in syringomyelia). Thus there may be loss of sensation of pain, heat and cold, with retention of the sense of touch over a segmental sensory area.

5. **Sensory Path in the Brain.**

It is most unusual for the sensory fibres alone to be involved.

(*a*) *Thalamus.*

(Usually the internal capsule is also affected.) There is complete anæsthesia and loss of emotional control.

(*b*) *Internal Capsule.*

(i.) A posterior limb lesion produces the same effects as (*a*), and in addition there is interference with the optic and auditory radiations (if the lesion extends sufficiently far back), so that sight and hearing are affected. There is blindness of the homolateral half of each retina.

(ii.) An anterior limb lesion causes the thalamus to be completely cut off from the cortex (see Part II., Chapter I.), except for the sensory relays for smell, taste, sight and hearing, the latter being bilaterally represented in the cortex.

6. **Sensory Cortex.**

The sensory cortex is more extensive than the postero-Rolandic convolution, and is concerned with intensity, localisation, discrimination, similarity and difference of stimuli, and also with stereognosis. Consequently the loss of function will correspond with the situation and the extent of the lesion concerned.

CHAPTER III

VISUAL PATH AND INTERFERENCE THEREWITH

For the anatomical course of the visual fibres the student is referred to Part I., Chapter VI.

(See Diagram 17, *facing* p. 18.)

It is important to emphasise that the image of any object situated on the temporal side of an eye falls on the nasal half of the retina of that eye. Similarly, an object situated on the nasal side of the eye produces an image on the temporal half of the retina of that eye. This, of course, only holds good if the object is not obscured from view by the nose. Consequently it is obvious that a distinction must always be made between the temporal half of the retina and the temporal field of vision. Images in the temporal field of vision will fall on the nasal half of the retina.

(See Diagram 38.)

Lesions of the Path.

The results of interference with the visual path at different levels between the periphery and the cortex are here considered, no distinction being made between the different pathological conditions which may cause the lesion ; a few of these only are mentioned to serve as illustrations.

(*a*) *Ganglion Cells of the Retina.*

There is loss of the field of vision corresponding to the area involved.

(*b*) *Optic Nerve.*

There is—

1. Blindness of the eye on the same side.
2. Diminution of the field of vision on the same side.

(See Diagram 39.)

(*c*) *Optic Chiasma.*

1. A transverse lesion of the chiasma leads to complete blindness.
2. Pressure on the crossing fibres in the chiasma, such as occurs in a progressive pituitary tumour, causes bilateral diminution of the peripheral field of vision. This is known as bitemporal hemianopia.

(See Diagram 40.)

3. Pressure on the outer fibres of the chiasma causes a bilateral loss of the nasal fields of vision.

(See Diagram 41.)

(*d*) *Optic Tract.*

There is loss of the opposite field of vision, blindness of the

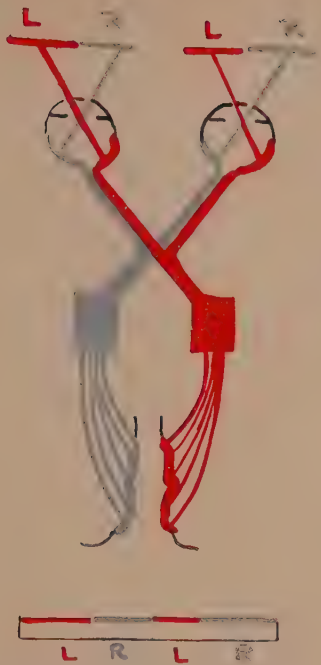

DIAGRAM 38.—Diagram of Field of Vision.

DIAGRAM 39.—Lesion of one Optic Nerve.

Effect on field of vision. Some diminution on side of lesion.

DIAGRAM 40.—Lesion of Crossing Fibres of Optic Chiasma.

Effect on field of vision. Bilateral diminution of peripheral field of vision.

DIAGRAM 41.—Lesion of Outer Fibres of Optic Chiasma.

Effect on field of vision. Bilateral loss of nasal fields of vision.

DIAGRAM 42.—Lesion of Optic Tract.

Effect on field of vision. Loss of field of vision on opposite side.

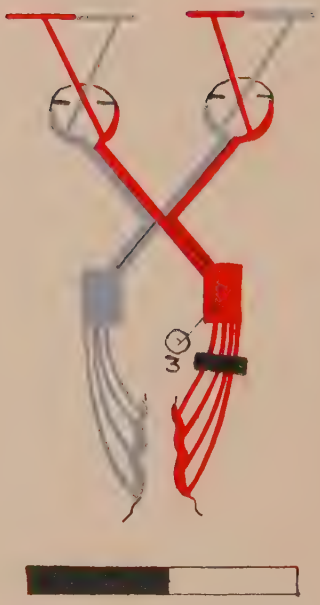

DIAGRAM 43.—Lesion of Optic Radiation.

Effect on field of vision. Loss of field of vision on opposite side. Light reflex unaffected.

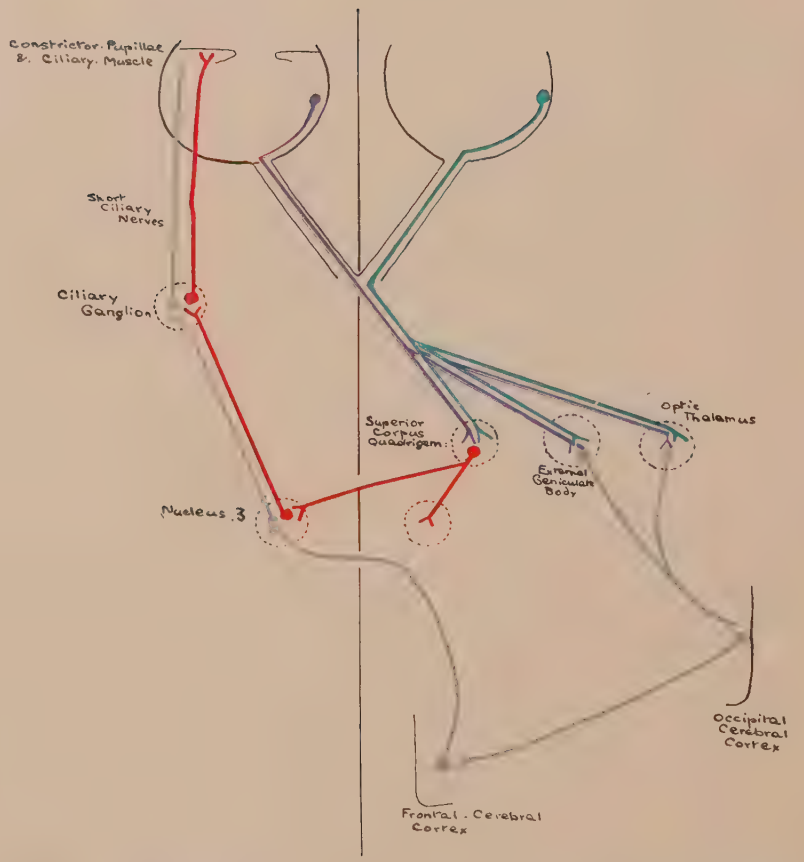

DIAGRAM 44.—Diagram to show Paths for the Light Reflex and for Accommodation.
Blue : Accommodation path. Red : Light reflex path.

nasal half of the opposite retina and the temporal half of the retina of the same side.

(See Diagram 42.)

(*e*) *Optic Radiation or Occipital Lobe.*

The result is the same as that occurring in a lesion of the optic tract, except that the light reflex is intact.

(See Diagram 43.)

[NOTE.—As there is some ambiguity in the use of certain terms in connection with vision, the following list of terms, with their meaning, is given :—

Hemiopsia	Presence of half the field of vision.
Hemianopsia	Loss of half the field of vision.
Hemiopia	Half-sight.
Hemianopia	Half-blindness.]

Accommodation Reaction.

The pathway of accommodation is from the occipital lobe, which receives the afferent impulses from the retina, to the frontal cortex. From this cortex the fibres run through the genu of the internal capsule and the medial part of the crusta to the nucleus of the opposite third nerve. Axons from the third nucleus pass to the constrictor pupillæ muscle and the ciliary muscle through the ciliary ganglion. It will be noted that the superior corpus quadrigeminum does not lie on this pathway.

(See Diagram 44.)

Light Reflex.

The pathway of the light reflex passes from the retina by specially thick fibres (Monakow) in the optic tracts to the superior corpus quadrigeminum. The next relay arises in the corpus, and crossing the mid-line by fibres both anterior and posterior to the Sylvian aqueduct, reaches the front part of the nucleus of the third nerve. From this nucleus fibres are relayed in the ciliary ganglion, and so reach the eye *viâ* the short ciliary nerves. It will be noted that fibres from each retina reach both optic tracts and also both superior corpora quadrigemina, so that light shining on one eye causes constriction of both pupils. This constitutes the " consensual light reflex."

The following reactions are used so commonly that a short description of the anatomical pathway taken by them is given :—

I. *The Argyll-Robertson Pupil.*

In this the light reflex is lost, but the accommodation reflex is intact. It is due to a lesion in the neighbourhood of the Sylvian aqueduct (involving the connections between the two superior corpora quadrigemina by the posterior commissure), or to a lesion of the pathway between the superior corpora quadrigemina and the third nerve nucleus, or of the ciliary ganglion.

II. *Wernicke's Pupillary Reaction.*

In this the light reflex remains, although sight is lost, due to a lesion in the optic radiation, or in the higher visual centres in the cortex, thus not affecting the superior corpus quadrigeminum.

CHAPTER IV

THE COCHLEAR PATH AND THE OLFACTORY PATH AND INTERFERENCE THEREWITH

Interference with the Cochlear Path.

For the anatomical course of the cochlear division of the eighth nerve reference may be made to Part I., Chapter VI.

(See Diagram 23, *facing* p. 21.)

1. Destruction of the cells of the upper part of the cochlea produces deafness to low notes, while destruction of the cells of the lower part of the cochlea produces deafness to high notes.

(See Diagram 45.)

2. (*a*) An irritative lesion on the peripheral path of the cochlear nerve causes tinnitus on that side.
   (*b*) A destructive lesion of the peripheral path causes complete deafness on that side.
3. Unilateral destruction of the temporal lobe does not cause complete deafness on that side, as both cochleæ are represented in both temporal lobes.

The effects of interference with the connections of the auditory centre are further discussed in connection with the condition of "Aphasia," Part II., Chapter X.

Interference with the Olfactory Path.

As the sense of smell subserves the needs of the human organism to such a small extent in comparison with the importance of this function in some animals, the results of interference with the olfactory path are relatively few and unimportant. It must also be remembered that it is difficult in man to dissociate smell from taste, and *vice versâ*, the two senses being intimately associated.

1. Destruction of the cells of the olfactory epithelium leads to loss of smell.
2. Lesions of the pyriform area lead to subjective sensations of smell.

(See Diagram 15, *fncing* p. 18.)

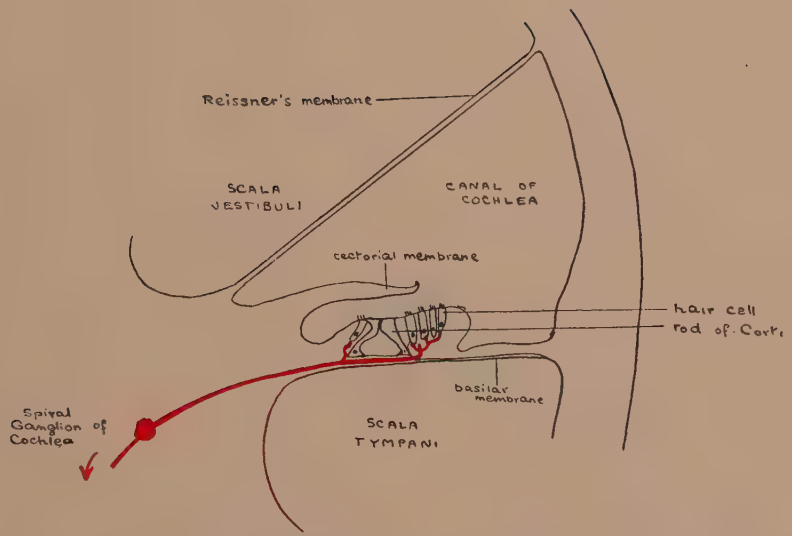

DIAGRAM 45.—Diagram to show Origin of Cochlear Nerve Fibres among Hair Cells of Organ of Corti.

CHAPTER V

THE CEREBRAL CORTEX

THE structure of the cerebral cortex has been described in Part I., Chapter VIII.

Significance of the Cortical Layers.

1. Outer cell lamina, of small pyramidal cells.
   (*a*) This layer is the last to develop in man, and is the first to be affected by disease.
   (*b*) The degree of development of this layer is increased as the animal scale is ascended.
   (*c*) Its thickness varies directly with the mental capacity of the individual.
   (*d*) If this layer is congenitally deficient, amentia results.
   (*e*) Degenerative changes in this layer are associated with dementias.
2. Middle cell lamina, of granule cells.
   (*a*) This layer is thickest in the post-Rolandic area and part of the occipital and temporal lobes.
3. Inner fibre lamina.
   (*a*) This layer contains the giant motor cells (Betz cells) in the pre-Rolandic area only.
4. Inner cell lamina, of polymorphous cells.
   (*a*) This layer is the first to develop in man.
   (*b*) It does not increase in thickness in man after birth, and is of constant depth throughout the cerebral cortex.
   (*c*) It is relatively thick and well developed in lower animals.
   (*d*) It is the last layer to be affected in disease. It shows marked decrease in aments, and also in gross dements who cannot carry on the ordinary functions of life.

From the foregoing observations it is concluded that these cell layers have the following functions :—

1. The outer cell layer subserves the higher functions of memory and the higher intellectual and moral qualities.
2. The middle cell layer is concerned with receiving afferent impressions from the lower sensory neurones or from other regions of the cerebrum.
3. The inner cell layer carries out the lower voluntary and instinctive activities involved in the maintenance of life and species.

The Localisation of Function in the Cerebral Cortex.

Historical.

One of the first attempts to localise any particular function in any special area of the brain was due to a phrenologist, Gall, in 1810. He ascribed consciousness to the cerebral hemispheres, and endeavoured to correlate the appearance of the inside of the skull with the appearance of the brain that originally occupied it and the characteristics of the individual to whom it had belonged. As a result he drew up elaborate brain maps ascribing various characters to different parts of the brain. In 1824 Flourens carried out some experiments, removing the cerebral hemispheres in small portions, and he found that at first there was no change; then the animal became dull and stupid, and then unintelligent all at once. He found no difference for different parts of the brain, the result depending only on the amount of tissue removed. He concluded that there was no localisation, but that the brain was functionally equivalent in all its parts.

This doctrine was undisputed until in 1861 Broca made the observation that loss of speech is frequently associated with a lesion of a definite spot. This area, known as Broca's area, was consequently for many years regarded as the seat of the function of speech. In 1864 Hughlings Jackson observed that localised muscle spasms are connected with lesions of certain parts of the central convolutions, to which were therefore ascribed motor functions.

Another and very promising method of investigation was introduced in 1870 by Hitzig and Fritsch, who made use of dogs. They observed the effects of weak faradic excitation of different parts of the exposed cortex; definite co-ordinated movements of muscle groups were produced by pre-central stimulation, and these workers drew up plans of the brain ascribing definite functions to various regions. This work was repeated in 1873 by Ferrier, and he confirmed the results in monkeys. He showed also that removal of these motor areas resulted in loss of volitional initiation of movement.

Since this time the work has been frequently repeated and extended to the higher apes, and even to man, by Horsley, Schafer, Sherrington, and others. Recently Head has made confirmatory observations on men in whom part of the cortex had been exposed by gunshot wounds.

Evidence as to the Localisation of Function in the Cerebral Cortex.

The information obtained from all methods of investigation must be considered together. There are four methods that yield contributory evidence :—

1. Structure.
   - (*a*) Gross, comparing different animals.
   - (*b*) Minute.
2. Stimulation.
   - (*a*) Experimental.
   - (*b*) Pathological—*i.e.*, an irritative lesion, such as a tumour producing over-action of the part pressed on.

3. Destruction.
   (*a*) Experimental.
   (*b*) Pathological—*i.e.*, a destructive lesion, causing replacement of tissue by a pathological process such as a tumour.
4. Flechsig's myelination method.

Considering the evidence of each of these methods in turn, the following information is obtained :—

1. Structure.

(*a*) *Gross.*—The gross structure of the brain varies greatly in different animals, the relative development of the olfactory lobes, optic lobes, cerebellum, and cerebral hemispheres varying with the relative degree of development in the animal of that function which (from other sources of evidence) is ascribed to that particular part. Thus in fishes the olfactory lobes are enormously developed, and are much more highly differentiated in animals low in the vertebrate scale than in those higher up. The optic lobes are exceedingly prominent in birds, in which the sense of sight is greatly specialised. Many other examples of this principle can be found.

(*b*) *Minute.*—The minute structure of the cortex has already been described, including the variations in different parts of the brain. These variations, considered in conjunction with the functions of the different layers just described, throw considerable light on the localisation of function in the different parts of the cortex.

2. Stimulation.

(*a*) *Experimental.*—The unipolar method of electrical stimulation is used, because by this means it is possible to localise the stimulus very precisely, and also to use a stimulus of known strength which can be varied or repeated as required. Weak stimulation of a motor area always gives an immediate motor response, but a certain amount of irradiation always occurs, so that the motor response is out of proportion to the area to which the stimulus is applied. Stimulation of the sensory areas is unsatisfactory, as in animals sensory effects cannot be detected by the observer, and an intense stimulus is necessary to produce even a slight motor response of the corresponding region. Stimulation of other areas of the cortex gives rise to no response, and these are consequently known as " silent areas."

(*b*) *Pathological.*—Irritation of the motor cortex caused by some pathological process produces the Jacksonian type of epilepsy. This is characterised by a definite sequence of movements which are " fired off " by the cortical stimulus that causes the initial movement. Thus the movements always begin in the same part of the body, and this corresponds to the cortical area that is being stimulated ; the movements then spread always in a definite sequence. It should be noted

that movements rather than muscles are represented in the cortex. The evidence so obtained was confirmed and extended by the observations of Head and Riddoch on the effects of gunshot wounds.

3. Destruction.

(*a*) *Experimental.*—Removal of a motor area causes loss of voluntary movement in the area represented. Similarly, removal of a sensory area involves loss of the sensation concerned. The degree of recovery depends on the capacity of other parts of the brain to take on the

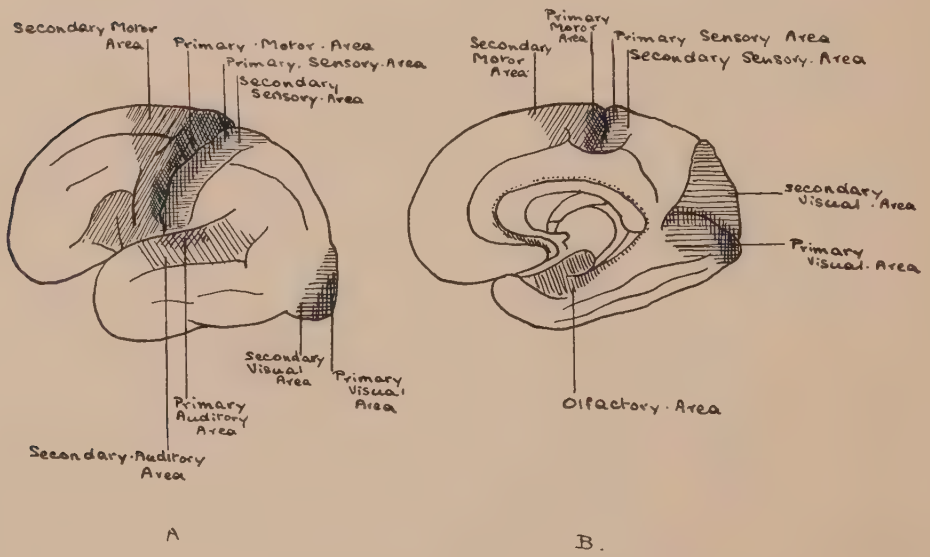

Diagram 46.—Campbell's cortical projection areas.

A. Lateral aspect of cerebral hemisphere. B. Medial aspect of cerebral hemisphere. (*After Ranson.*)

function of the part removed; there is no regeneration of cerebral nervous tissue.

(*b*) *Pathological.*—The results of some pathological conditions are difficult of interpretation because a tumour may cause destruction of one part and simultaneous irritation of another, so that the results are not usually very localised. Further confirmation is afforded by war injuries.

4. Myelination.

The date of myelination of nerve fibres coincides with the taking on of function. Thus the sensory paths myelinate early, the column of Goll at five to five and a half months of fœtal life, and the column of Burdach at the beginning of the eighth month of fœtal development. The motor tracts myelinate later,

the pyramidal tracts being fully developed only two years after birth. The association tracts myelinate last of all.

Evaluation of Evidence.

Evidence obtained by the foregoing methods shows clearly that certain functions are associated with certain areas of the cerebral cortex, and it is possible to distinguish definite motor and sensory areas, the remaining cortical tissue being designated as silent or association areas. Since volitional motor impulses never arise spontaneously in the pyramidal cells, but activity is determined by afferent impressions, there must be a close relation between the afferent and efferent neurones.

A motor area is controlled by and closely associated with the region in which are stored the memories of its previous activities, such an area being spoken of as a kinæsthetic area (κινέω (to move) and αἴσθησις (sensation)). Similarly, a sensory area is closely associated with the region in which are stored the memories

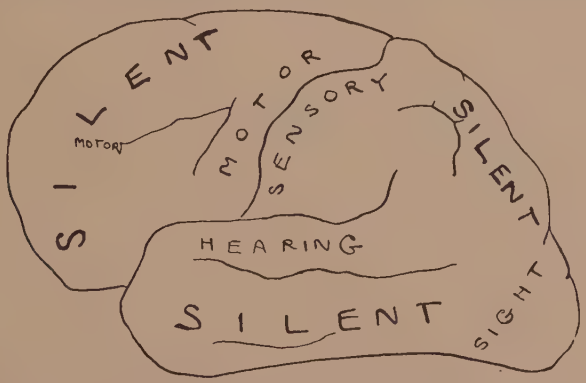

DIAGRAM 47.—Diagram to show " silent " or " association " areas of cerebral cortex.

of previous impressions reaching this sensory area, this being known as a sensory-psychic area. The part played by these kinæsthetic and psychic areas is well illustrated in the various types of aphasia (see Part II., Chapter X.).

(See Diagrams 46 and 47.)

A. Region in Front of the Rolandic Fissure.

(*a*) *Motor.*

(i.) Area for eye movements.

Stimulation of this area on the right side leads to conjugate deviation of both eyes to the left; hence these movements are bilaterally represented in the cortex. A further analysis of these movements will be found in Part II., Chapter IX.

(ii.) Pre-Rolandic area.

This area extends further than was originally described and includes primary and secondary voluntary motor centres,

the pyramidal fibres arising here. In these centres the limbs are contralaterally represented, but movements involving both sides, such as those of the head and trunk, are bilaterally represented. The bilaterality of response is not altered by extirpation of the cortex of the hemisphere opposite to that being stimulated, so that interconnection must be at the lower motor levels.

(*b*) *Association or Silent.*

The function of this area has been elucidated by congenital deficiency, degenerative disease, and accidental destruction. The higher moral and intellectual qualities are usually assigned to this area, and this is exemplified by the well-known case of the crowbar accident to the American miner. The fronto-pontine cerebellar fibres arise here.

B. **Region Posterior to the Rolandic Fissure** (as in diagram).

(*a*) *Sensory.*

This area includes primary and secondary sensory centres, and the localisation of function is not very accurate.

(*b*) *Association or Silent.*

These regions are of a lower type than those described above.

C. **Occipital Region.**

(*a*) *Sensory.*

(i.) Visuosensory.

This consists of the region round the calcarine fissure on the medial and extending on to the superior part of the hemisphere. In this area are received optic impulses, but they are not interpreted here (see Part II., Chapter II.). There is a special area for reception of macular impulses.

(ii.) Visuopsychic.

This is on the outer aspect of the occipital lobe, and is used for the storing of the memories of impulses reaching the visuosensory area. This area is consequently essential for the interpretation of such impulses.

(*b*) *Motor.*

There is a region at the occipital pole which on stimulation produces conjugate deviation of the eyes similar to that produced by stimulation of the eye area in the frontal region. (This is possibly explained by an interconnection between these two areas.)

(*c*) *Association.*

The occipito-pontine-cerebellar fibres arise here.

D. **Temporal Region.**

(*a*) *Sensory.*

(i.) Olfactory-sensory.—The uncus and pyriform area are concerned with smell.

(ii.) Auditory-sensory.—The anterior part of the superior temporal convolution receives auditory impulses.

(iii.) Auditory-psychic.—The auditory impressions are stored in the posterior part of the superior temporal convolution, and are therefore available for the interpretation of the auditory sensory impulses.

(*b*) *Association or Silent.*

The temporo-pontine-cerebellar fibres arise here.

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CHAPTER VI

THE NORMAL PHYSIOLOGY OF THE MOTOR PATH

It is improbable that motor acts are ever initiated spontaneously by the nervous system ; they occur as a response to some stimulus which sends afferent impulses to the cord or to the brain. The involuntary " fated " response that sometimes occurs is spoken of as a reflex response (see Part II., Chapter VIII.). But in many cases the response is determined by memories and associations of previous situations that are stored in the cerebral cortex, and in this case the response frequently appears quite unrelated to the stimulus ; such motor responses are usually spoken of as " voluntary." A " voluntary " movement, however, frequently includes components that are outside consciousness and might be termed involuntary. Many movements that are at first voluntary, requiring conscious attention, later become relegated to centres lower than the conscious " voluntary " cortex, and are carried out automatically. An example of such a movement is that of walking.

The impulses for voluntary movement are carried by the pyramidal paths arising in the pre-Rolandic cerebral cortex. These tracts are not completely myelinated until about two years after birth ; consequently the movements of the new-born baby are carried out by other motor paths, the extra-pyramidal system, which is developmentally an older path than is the pyramidal.

The Pyramidal Path.

The fibres of the pyramidal tracts are the axons of the Betz cells of the cerebral cortex, and are the longest nerve fibres in the body ; they pass straight down through the internal capsule, crusta, pons, and pyramids, to the cord, with no cell station until they reach the level at which the impulse is to pass out. The fibres then arborise round cells of the grey matter, and connector neurones distribute the impulse to many anterior horn cells, the stimulus ultimately passing out by many nerve fibres supplying the groups of muscles. Thus it is brought about that an impulse passing down the pyramidal fibres will produce, not the contraction of a certain muscle, but a " movement " involving many muscles. This point will be considered more fully in subsequent chapters.

The impulses passing down the pyramidal fibres can also control impulses from other sources converging on a lower motor neurone, and these modify or inhibit the response that would otherwise occur.

The Extra-pyramidal Paths.

This system includes the corpus striatum (*i.e.*, caudate nucleus and the two divisions of the lenticular nucleus, *i.e.*, globus pallidus and putamen), the red nucleus, substantia nigra, subthalamic nuclei and other nuclei of the tectal region

of the mid-brain, and the tracts arising directly from these or from nuclei receiving impulses from them, namely, the rubrospinal, tectospinal, pontospinal and vestibulospinal tracts.

Phylogenetically the globus pallidus is the oldest part of this system of nuclei, and its efferent fibres myelinate very early. The caudate nucleus and putamen are of more recent development and more highly specialised, and are both concerned with modifying the motor responses of the globus pallidus chiefly through the afferent thalamic impulses reaching them. Our knowledge of the functions of these nuclei is derived chiefly from a consideration of lesions involving the nuclei or their tracts, and may be briefly summarised here.

The caudate nucleus and the putamen regulate the motor responses of the globus pallidus. Afferent impulses are continually streaming up to the thalamus, many of which overflow into the efferent path through the globus pallidus giving rise to the forced involuntary movements. This overflow is prevented and controlled by the caudate nucleus and putamen.

The globus pallidus probably carries out many of the so-called automatic movements, which were originally mediated through the cerebral cortex, and from much use have become relegated to lower grade motor centres. It also exerts a controlling action on muscle tone. These muscle tone reflexes, which include the mechanism of neuromuscular rhythm, are normally carried out through the cerebellar—red nucleus—rubrospinal path, and these responses are controlled at the red nucleus level by impulses from the globus pallidus of the same side.

REFERENCE

KEILLER. " Anatomy and Physiology of the Nerve Tracts of the Brain and Cord," 1927, pp. 55 and 271 (Macmillan).

CHAPTER VII

RESULTS OF INTERFERENCE WITH THE MOTOR PATH AT VARIOUS LEVELS

This chapter should be read in conjunction with Part II., Chapter VI., which deals with the normal physiology of the motor path.

The results of destructive lesions at different levels in the motor path will now be considered, beginning at the cortex and working towards the periphery.

1. Cerebral Motor Cortex.

The effect of damage to the cerebral motor cortex is discussed in Part II., Chapter V., and will vary according to the part of the motor area involved.

2. Internal Capsule.

Since all pyramidal fibres are concentrated into a narrow band passing through the internal capsule, any lesion (such as hæmorrhage) is likely to involve a large part of the path. It must be noted that sensory involvement from such a lesion is usually small and readily clears up. Particular results depend on the exact position of the lesion, and which fibres are involved, the effects being always on the opposite side of the body.

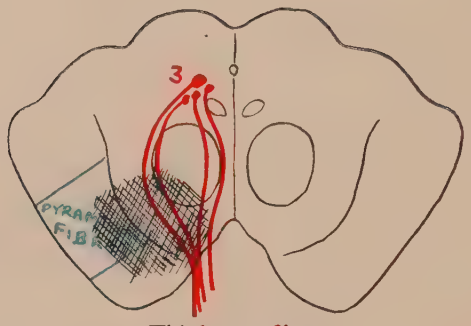
The most common lesion is due to hæmorrhage from the lenticulo-striate artery, and there is always some residual fibrosis from the clot. The occurrence is so frequent that a full account will be given.

(*a*) The muscles of the opposite side are flaccid and toneless; the deep reflexes are lost, even though these depend on the integrity of the brain stem and spinal cord reflex arcs, because in any severe lesion of the central nervous system function is disturbed, even in regions remote from the structures affected. The paralysis varies in different regions of the body; for example, the eye, chest and abdomen muscles are very slightly affected, while muscles which act bilaterally usually escape, because of the commissural fibres connecting their nuclei.

(*b*) Recovery may occur and be nearly complete after the initial stage of shock is over, and this is probably due to the improvement in the general circulation and to the removal of pressure from the fibres, for if the fibres are actually destroyed function in them clearly cannot be restored.

(*c*) Emotional movement has a separate pathway, and so remains unaltered.

(*d*) Certain reflexes can be aroused on the affected side from the normal side, and these are concerned with "associated movements," such as clenching the fist.



Pyramidal fibres supplying opposite side of body.

Third nerve fibres supplying eye of same side.

DIAGRAM 48.—Diagram to illustrate "Crossed Paralysis" due to a Lesion involving Pyramidal Fibres and a Cranial Motor Nerve.

It must be remembered that such a lesion may also involve the corpus striatum connections (see Part I., Chapter VII.).

The reader should also refer to the account of " Upper Motor Neurone Lesions " given in Part II., Chapter IX.

3. **Pyramidal Path in the Mid-brain.**

All pyramidal fibres are still uncrossed at this level ; hence the lesion affects the opposite side of the body.

Intracranial cerebral fibres of the cranial nerves may also be involved on account of their position. The third nerve is especially liable to be affected in this way, and as this is a lower motor neurone lesion, the effect will be on the same side of the body, thus producing a " crossed motor paralysis."

(See Diagram 48.)

4. **Pyramidal Path in the Pons.**

(i.) *Upper Pons.*—The results are the same as for the mid-brain, but the cranial nerve involved is the fifth.

(ii.) *Lower Pons.*—The sixth and seventh cranial nerves are usually involved in this lesion, and there is a " crossed motor paralysis." Since some or most of the upper motor neurone fibres of the facial nerve cross, a lesion extending upwards may involve both sides of the face.

5. **Pyramidal Path in the Medulla.**

There is—

(*a*) An upper motor neurone paralysis of the opposite side of the body, but the head escapes.

(*b*) A lower motor neurone paralysis due to involvement of the hypoglossal nerve of the same side, so that there is complete paralysis of one side of the tongue.

(*c*) Frequently some involvement of the eleventh nerve.

6. **Pyramidal Path in the Cord.**

Since all the direct pyramidal fibres cross by the mid-thoracic level, and all crossed pyramidal fibres cross in the medulla, it follows that a lesion involving half the cord above the mid-thoracic level will interfere with voluntary movement on both sides, and a lesion below this level will involve movement on the same side only.

7. **Motor Part of a Mixed Nerve.**

This is a lower motor neurone ; the reader is therefore referred to Part I., Chapter II., for an account of degeneration of a nerve.

EXTRA-PYRAMIDAL SYSTEM

The functions of these paths have been almost entirely worked out by observing the results of disease (Parkinson's disease, encephalitis lethargica, and progressive lenticular degeneration).

The reader is referred to Part I., Chapter VII., for an account of the basal ganglia connections.

Lesions of this system produce—

1. Rigidity.
2. Involuntary movement.
3. Disturbances of movement.

1. Rigidity.

This so-called "extra-pyramidal rigidity" must be differentiated from "pyramidal rigidity."

Pyramidal Rigidity.

(*a*) Is usually hemiplegic.
(*b*) Affects flexor muscles to a greater extent than the extensors.
(*c*) Produces the so-called "clasp-knife" effect.

Extra-pyramidal Rigidity.

(*a*) Is usually segmental in its effect.
(*b*) Is more marked proximally than distally.
(*c*) Produces the so-called "leaden pipe" rigidity.
(*d*) Produces cogwheel rigidity.

Extra-pyramidal rigidity can be abolished by the injection of cocaine into the rigid muscle. As this abolishes the sensitivity of sensory nerve endings, this suggests that striate rigidity is reflex in origin.

This rigidity affects both the agonists and the antagonists, giving a fixed position of flexion, and it may be so marked that voluntary movement becomes impossible, although the pyramidal path is intact.

There is a mask-like condition of the face, but the reflexes are unaffected until the rigidity is sufficient to prevent any reaction.

2. Involuntary Movement.

Tremor is usually the most marked involuntary movement, and has been described by Kinnier Wilson as "a fairly regular rhythmical alternating contraction of a muscular group or groups and their antagonists." Striate tremor shows a fairly constant rate (*i.e.*, six per second), but the range varies from very fine to coarse wide movements. The movements most commonly affected are in the distal parts of the body, *i.e.*, the fingers, hand, lips, or tongue.

The law of reciprocal innervation holds good (see Part II., Chapter IX.), and recent work seems to show that striate tremor may be due to the released activity of a centre, probably situated in the mid-brain.

3. Disturbances of Movement.

There is—

(*a*) Weakness of muscles, so that fatigue sets in more rapidly.
(*b*) Slowness, irregularity and limitation in extent of many movements, especially those made by the laryngeal and eye muscles. This

latter effect produces a jerky movement of the eyes on looking to one side. The small muscles of the limbs are also affected.

(*c*) Inability to maintain a contraction.

(*d*) A lack of movements of co-operation, which, together with a general poverty of movement, is probably due to the rigidity, ease of fatigue, and need for extra effort on the part of the patient to carry out a movement. Hence there is a tendency to avoid these movements, although there is no actual interference with the pyramidal path.

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WRIGHT. "Applied Physiology," 1926, pp. 55–57.

CHAPTER VIII

REFLEX ACTION

The term " reflex action " includes a stimulus, with its involuntary response. There is no essential difference between the voluntary response to an afferent impulse and the involuntary reflex response. In each case there must be an afferent impulse due to a stimulus (nervous or chemical) which is at some level brought into relation with the origin of efferent impulses. The reflex response in some cases arouses consciousness (*e.g.*, the watering of the eye due to the presence of a foreign body), but in many cases there is absolute unconsciousness of the reflex act in progress (*e.g.*, the opening of the ileocolic sphincter due to nervous impulses from the stomach).

The simplest anatomical arrangement whereby a stimulus may produce a definite motor response is known as the reflex arc, and in the nervous system of vertebrates the reflex arc consists of three neurones. There is—

1. The afferent or receptor neurone, consisting of the specialised ending of dendrites for receiving the stimulus, the nerve cell in the posterior root ganglion, and its axon passing into the cord by the posterior root and arborising in the grey matter.
2. The connector neurone in the grey matter, whose axon arborises round the dendrites of an anterior horn cell.
3. The efferent or effector neurone, consisting of the anterior horn cell, with its axon passing out to the organ of response (see Diagram 49).

The simplest reflex arc is the one involving posterior and anterior root fibres and cord connections at one level, but the integration of the afferent impulse with the efferent impulse can occur at many levels, such as the medulla, cerebellum and mid-brain. At every synapse it is possible for other nervous impulses to enter and modify the response, and consequently the real characteristics of a purely reflex act frequently become obscured. In order to study the pure reflex it is necessary to prevent impulses from higher centres from reaching the level at which the integration is occurring, and for this reason the " spinal " animal is used, *i.e.*, one in which the cord is severed from the medulla, and the spinal reflexes can be studied.

A. Reflexes in the Spinal Frog.

If the cord is cut just below the medulla, the animal passes at once into the condition known as " spinal shock." It lies flat and motionless, with the limbs completely flaccid, and gives no reaction to stimuli. After about ten minutes the condition of shock begins to pass off, the muscles resume their condition of tone,

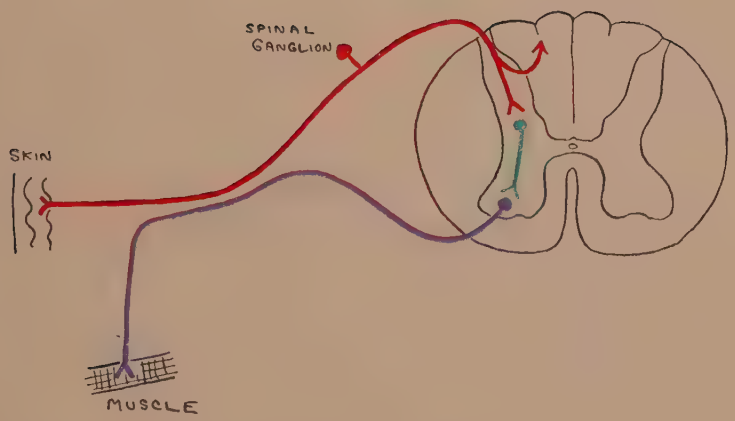

DIAGRAM 49.—Diagram of Simple Reflex Arc as present in the Spinal Cord.

Red : Receptor neurone.
Green : Connector neurone.
Mauve : Effector neurone.

and the animal assumes the normal squatting posture. It will then respond to stimuli in the usual way. If placed at the foot of an inclined board, it will hop to the top and sit there; if placed in water, it will swim. If a drop of weak acid is placed on the flank, the frog will try to wipe it off with the corresponding leg; if this leg is held, it will use the opposite one. The stronger the stimulus used the more rapid is the response. These few examples serve to show the protective nature of these spinal reflexes, and also the purposeful character of the response. The response evoked is directly related in kind and in degree to the stimulus, and it is possible to predict what will be the response to any given stimulus. In the spinal animal the reflex response is a "fatal" one, *i.e.*, it must always be the same for any one stimulus; in the intact animal the "fatal" response may be modified by impulses from higher centres.

By "reaction time" is meant the time that elapses between the giving of the stimulus and the response, and this will depend upon the synapse. A nerve impulse travels very rapidly along a nerve fibre, but much more slowly across a synapse; thus the condition of the synapse can affect the reaction time to a marked degree. The passage of a nerve impulse is delayed by conditions that impede its passing across this junction; for example, bromides and chloroform increase the resistance at the synapse, and therefore increase the reaction time. On the other hand, the resistance at the synapse may be lowered; if this occurs to any marked extent (as in strychnine poisoning), the nerve impulse will spread to adjacent neurones, and the response loses its local purposive character and becomes widespread. This "reflex spread," or irradiation, is the cause of strychnine convulsions.

B. **Reflexes in the Spinal Dog.**

The immediate effect of section of the cord just below the medulla is again one of "spinal shock," with complete loss of tone and loss of response to stimuli. After several days the condition of shock wears off and muscle tone returns. The animal can then take a few steps if raised and given a push forwards, and certain reflex movements are carried out. Reflex emptying of the bladder and rectum takes place, pregnancy with a normal parturition is possible, and the scratch reflex, flexor reflex and extensor or stepping reflex are easily elicited.

C. **Reflexes in Spinal Man.**

The immediate condition of spinal shock with complete flaccidity of muscles lasts for sixteen days or more; if sepsis should supervene, the condition of shock lasts longer. Reflex (or automatic) emptying of the bladder and rectum then returns with the return of muscle tone, but other spinal reflexes below the level of the lesion tend to lose their local significance and become "mass reflexes." Thus any afferent stimulus below the lesion may provoke diffuse and widespread sweating and premature evacuation of the bladder. These mass reflex responses may result from such a stimulus as scratching the sole of the foot.

From a consideration of these examples it is seen that the chief characteristic of reflex actions is their protective nature; originally the response was one

necessary for life. The reflex response is rapid and purposeful in nature, being limited to the needs of the stimulus. If impulses from other sources can be excluded, it is usually possible to predict the response that will occur to any given stimulus. But as the animal scale is ascended the functions of the spinal cord become more and more subservient to those of the cerebral cortex, and consequently the range and degree of development of the pure spinal reflex becomes less.

Inhibition of the Reflex Response.

The involuntary response of the reflex can be inhibited under certain conditions.

(*a*) *Chemical Inhibition.*

If a crystal of salt is placed on the distal cut end of the spinal cord, all spinal reflexes are inhibited.

(*b*) *Voluntary Inhibition.*

Within certain limits it is possible by an effort of will to inhibit the reflex responses to some stimuli.

(*c*) *Inhibition by a Stronger Sensory Stimulus.*

If a stronger sensory stimulus is applied simultaneously with the original stimulus, the reflex response to the original stimulus is frequently inhibited. For example, yawning or sneezing can be prevented by firm pressure or pinching of the skin of the bridge of the nose or upper lip.

(*d*) *Inhibition by a Hurtful Stimulus.*

If a hurtful stimulus is applied, any reflex response to another stimulus that may be in progress is inhibited, so that the protective response to the harmful stimulus may take place. For example, if the scratch reflex is elicited in a dog, and during its progress the foot is pricked, immediately there is a flexor reflex response and inhibition of the scratch reflex. A hurtful stimulus is always the preponderant one, this type of inhibition being spoken of as "inhibition by nociceptive stimuli." It is clear that two reflexes cannot occupy the same nerve path at the same time, and since there is only one "final common path" from the spinal cord to any one muscle, it is necessary that one impulse should receive preference; this preference is always accorded to the protective impulse which is the reflex response to the hurtful stimulus.

Facilitation of the Reflex Response.

It sometimes happens that a small stimulus produces an impulse which is insufficient to pass across the synapse and produce a response. In such a case repetition of such small stimuli will ultimately produce a response. The initial impulse is not strong enough to pass across the synapse, but it does nevertheless produce a physico-chemical change. The final result of a series of such impulses is to bring about physico-chemical changes sufficient to carry the impulse across the synapse to the next neurone, and so bring about a response. The reflex

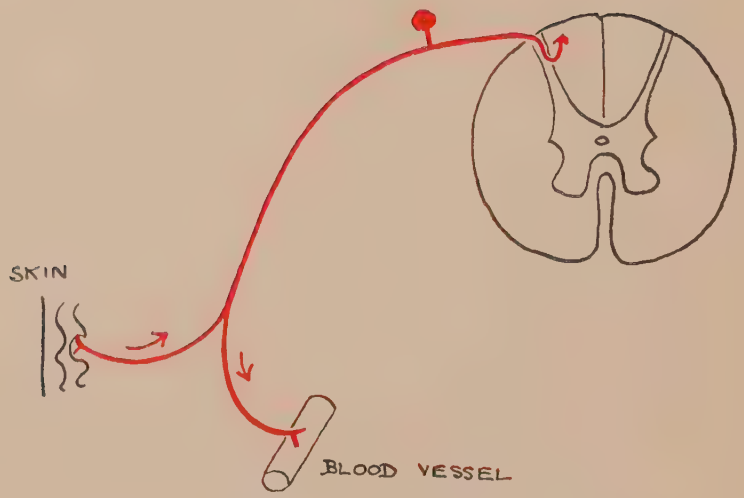

DIAGRAM 50.—Diagram to illustrate Axon Reflex of Skin.

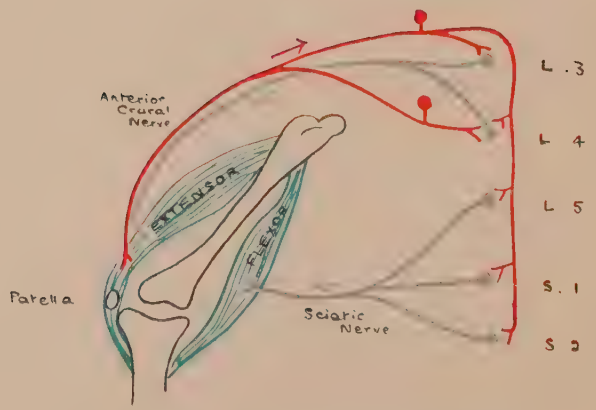

DIAGRAM 51.—Diagram to illustrate the Knee Jerk.

response is also facilitated by frequency of elicitation ; in other words, if a particular reflex arc is used frequently, the reaction time involved in its use is decreased. This is the basis of habit formation, and must be due again to some change at the synapses between the neurones involved.

The Axon Reflex.

If the posterior root fibres are cut, stimulation of the peripheral end of the cut nerve root produces vasodilatation of the cutaneous blood vessels. If a stimulant such as mustard is applied to the skin, the cutaneous vasodilatation again occurs. The reflex path involved consists of the sensory nerve ending in the skin, the sensory nerve fibre and the collaterals of this nerve fibre to the blood vessels (see Diagram 50). This is an example of a very rapid local protective mechanism, the impulse not passing through any nerve cells.

Types of Reflexes in Man.

The reflexes are usually divided into three groups :—

(A) Superficial or skin reflexes—*e.g.*, the plantar and epigastric reflexes.

(B) Tendon reflexes—*e.g.*, the knee jerk.

(C) Deep or visceral reflexes—*e.g.*, micturition.

(A) *The Plantar Reflex.*

If the outer side of the sole of the foot is stimulated, the big toe moves downwards—*i.e.*, a flexor response. In children up to two years and in cases of disease of the pyramidal tracts, this stimulus causes an upward stretching of the big toe—*i.e.*, an extensor response. The extensor plantar reflex is a purely spinal one, the flexor response being due to cerebral activities through the pyramidal fibres. An extensor response after two years of age is known as the Babinski phenomenon, and hysterical paralysis with the flexor plantar reflex can thus be distinguished from pyramidal paralysis with the extensor response. The reflex depends upon the integrity of the spinal centres at the levels of L. 5, S. 1 and S. 2.

The Epigastric Reflex.

If the skin is stroked beneath the breast, there is retraction of the body wall in the middle line. This reflex is of most diagnostic importance in cases of hemiplegia where comparison can be made with the normal side ; in bilateral lesions the reflex is uncertain.

(B) *The Knee Jerk.*

If the patellar tendon is tapped with the hamstring muscles relaxed, there is contraction of the extensors and relaxation of the flexors, resulting in the upward kick of the leg. The normal response varies considerably, but certain conditions affect the movement in a very definite way (see Diagram 51).

(i.) *Loss of Knee Jerk.*—This may be due to—

(*a*) Interference with the reflex arc.

1. Division of anterior crural nerve.

2. Division of anterior or posterior (*e.g.*, locomotor ataxy) nerve roots, L. 3 or 4.
3. Destruction of anterior horn cells at level L. 3 or 4 (*e.g.*, anterior poliomyelitis).

(*b*) Shock from complete section of the spinal cord. (The reflex then seldom returns except in lower animals.)

(*c*) Increased inhibition of the antagonist muscles, due to stimulation through the sciatic nerve.

(*d*) Interference with the anatomical paths connected with the maintenance of muscle tone, particularly the posterior column fibres.

(*e*) Sleep.

(ii.) *Increase of Knee Jerk.*—This may be due to—

(*a*) Removal of impulses from the cerebrum and consequent increased reflex excitability of the lower spinal centres—*i.e.*, an upper motor neurone lesion, such as injury to cerebral cortex or pyramidal tracts. The reflex excitability may be so greatly increased that a single stimulus evokes a clonic response—*i.e.*, a series of contractions and relaxations. (This clonus is obtained in the case of the ankle jerk more readily than in the knee jerk.)

(*b*) Hyperexcitability of the nervous system, as in hysteria.

(*c*) Action of drugs, such as strychnine, which lower the resistance at the synapse.

(*d*) Voluntary reinforcement by a simultaneous strong voluntary contraction. This is due to the concentration of cerebral control into the distracting voluntary action and consequent diminution of cerebral inhibition of the reflex. (Some writers explain reinforcement as due to general increased motor irritability produced by overflow from the voluntary motor activity.)

(*e*) Division of the sciatic nerve and consequent removal of the action of the antagonist muscle.

(C) *Micturition.*

Micturition was originally a reflex carried out by a centre in the lumbar cord. The afferent path from the bladder is by the nervi erigentes and pudic nerve, and the efferent path to the bladder by these same nerves ; the inhibitor path is by the hypogastric nerve (see Part I., Chapter X.). The normal stimulus for the reflex is a rise of pressure in the bladder due to the presence of urine. When cerebral control has been developed this reflex is subconsciously inhibited unless overridden by afferent stimuli ; the cerebral control can also be voluntarily removed.

According to Barrington, there are many factors concerned in the mechanism of voluntary micturition, including a higher centre in the pons. He found that in a decerebrate animal the following sequence occurred :—

1. Distension of the bladder, which produced strong contraction of the bladder wall.

2. This caused the presence of fluid in the urethra.
3. This distension of the posterior urethra produced a feeble contraction of the bladder.
4. The passage of fluid through the urethra reflexly inhibited the sphincter.
5. The bladder contracted and caused reflex relaxation of the urethra.

In the spinal animal the contraction of the bladder (1 and 3) did not occur; these responses are therefore carried out by a long reflex arc, of which the centre was found to be in the pons. The spinal cord is concerned only with the inhibition of the sphincter. This is supported by the observation that in spinal man contraction of the bladder is produced by reflex relaxation of the sphincter and spasm of the abdominal muscles.

Conditioned Reflexes

In addition to the unconditioned reflexes or " instincts " just described, there is a series of reflexes which are not inborn, but are acquired, and to which Pavlov has given the name of " conditioned reflexes."

These conditioned reflexes are only found when the cerebral cortex is existent, and are subject to inhibition as the result of many extraneous circumstances. It is the intrusion of such a variety of inhibitory influences that makes the actions of the cerebral cortex so involved. These reflexes have only recently been scientifically investigated, and the method used has been to build up in normal animals reflexes which can be evoked with the same certainty and measured with the same accuracy as can the reflexes in a spinal animal.

Law governing the Formation of Acquired Reflexes.

" Stimulation of any receptor organ occurring simultaneously with reflex excitation of an effector organ leads to the formation of a new reflex." These acquired reflexes can only develop on the basis of another existent reflex, which may itself be unconditioned or may be another conditioned reflex. Conditioned reflexes have been established with respect to the vasomotor system, glandular secretion, the heart, pupils, muscular movements, micturition, and so on. Their formation is due to the fact that " if a given receptor organ is stimulated during the occurrence of any original unconditioned or inborn reflex, a new link, a new nervous path, is formed between new receptors and the effector organ."

Most of Pavlov's investigations have been carried out by using the parotid salivary gland in the dog as the *effector* organ. An accurate quantitative measurement of the saliva secreted can be made, and sound has been used to form the conditioned reflex. Fundamentally there must be the simultaneous application of the original *neutral* stimulus and of any other stimulus which elicits ordinary reflex activity.

Consequently a conditioned reflex is built up in the dog by sounding a bell when food is brought into the animal's chamber. When the reflex is properly established the animal will salivate at the sound of the bell (conditioned stimulus),

even though the food (representing the unconditioned stimulus) may not be brought in. There are three types of conditioned reflexes: simultaneous, delayed, and trace. The rate of formation of these different types varies, simultaneous ones being formed much more quickly than are the delayed or the trace variety. The rate of formation is also dependent largely on the intensity of the conditioned stimulus employed, and there is an optimum intensity for every reflex, while discontinuous conditioned stimuli always produce a more rapid formation of acquired reflexes.

Properties of Conditioned Reflexes.

1. *Summation.*
   This is shown by the fact that if an animal stimulated with the smell of camphor produces sixty drops of saliva, and stimulated electrically yields thirty drops, it produces ninety drops when the two stimuli (camphor and electricity) are applied together.
2. *Specificity.*
   When a conditioned reflex is firmly established its specificity is increased.
3. *Stability.*
   To maintain the strength of any conditioned reflex, it must be regularly reinforced by the unconditioned stimulus.
4. *Experimental Extinction.*
   A conditioned reflex can quickly be extinguished if it is applied on several occasions without the accompaniment of the unconditioned stimulus.
5. *Irradiation.*
   (*a*) With simultaneous reflexes irradiation is only seen before the conditioned reflex is very firmly established. Once this has been accomplished, the area of irradiation is reduced to a small point round the original position; consequently the reflex is nearly specific within the same receptor organ.
   (*b*) With delayed type reflexes, however long the latent period may be, they always culminate in strictly localised reflexes.
   (*c*) With trace reflexes irradiation is much more extensive.
6. *Discrimination.*
   This is the function of the central nervous system, and discrimination can be made between very closely related stimuli, dividing them into effective and ineffective.

Pavlov has given the name of " analyser " to the entire mechanism comprising those parts of the central nervous and peripheral nervous systems which are related to each particular receptor organ. Probably analysis is mainly carried out in the cerebral cortex, and in this region too are developed new sets of conditioned reflexes. This latter function is known as its " synthetic activity." It must be noted that a single conditioned reflex can be extinguished without producing any effect on any other reflex, and that the specificity of conditioned reflexes, even within *one* receptor, is not perfect.

Auditory, visual, cutaneous and other senses may be used as analysers of conditioned reflexes, and a varying range of appropriate stimuli serves the purpose of building up very complicated conditioned reflexes. Discrimination of rate of vibration and of pitch is more accurate in the dog than in man, but visual stimuli are more perfectly estimated by the latter. Tactile stimuli and those of smell, muscle sense and pain can also be used for the formation of widely varying conditioned reflexes.

Inhibition of Conditioned Reflexes.

Inhibition of a conditioned reflex is only of temporary duration, and if an extraneous stimulus is repeated, its inhibitory effect decreases markedly and eventually disappears. Inhibition can be produced by any kind of stimulus affecting the central nervous system, provided that this stimulus is applied during or shortly before the occurrence of a conditioned reflex. This type of inhibition is known as *external*, and does not require any development of adaptation on the part of the animal. *Internal* inhibition, however, causes a previously effective stimulus to become ineffective, and is apparently due to an active condition of acquired inhibition.

Conditioned reflexes of higher orders may be established on the basis of other conditioned reflexes, and this includes both excitor and inhibitor types of response.

Localisation of Conditioned Reflexes.

The cerebral cortex is absolutely essential for the establishment of these reflexes. Local damage to the cortex has only a temporary effect on the reflexes, but more extensive injury leads to a permanent weakening of the inhibitory process, even though the reflexes themselves are still present. No single place in the cortex has been found which when extirpated leads to the abolition of all conditioned reflexes ; in most cases the centre for any given conditioned reflex corresponds practically with the anatomical cortical area associated with the particular analyser concerned. In higher animals localisation of the analysers is more precise than in lower animals, and the seat of inhibition is within the inhibited analyser, and not within the inhibiting one.

Sleep.

" This may be regarded as an accumulation of internal inhibitions, which is not concentrated merely within one analyser, but spreads over the whole cortical and subcortical areas." Similarly a lack of adequate inhibition for any particular process leads to a state of widespread excitation, but unless the general conditions alter, both conditioned excitor and inhibitor reflexes are extremely stable.

Effect of Altered Conditions.

(*a*) Digestive troubles lead to a temporary weakness and then to the abolition of the reflexes.

(*b*) Pregnancy and inanition cause a marked diminution of the reflexes, but they return to normal soon after delivery.

(*c*) Cretins show definite inability to develop any discrimination, and in them it is difficult to establish any kind of conditioned reflex.

(*d*) In the young conditioned reflexes are more quickly acquired than in the aged, but once the reflex is established in youth, it persists to the end of life.

(*e*) In successive generations each generation acquires a particular reflex after fewer trials than did the preceding generation.

(*f*) Drugs have a definite effect on these reflexes. Caffeine augments the reflex and at the same time diminishes every inhibitory process, while bromides increase the inhibitory power of the cortex.

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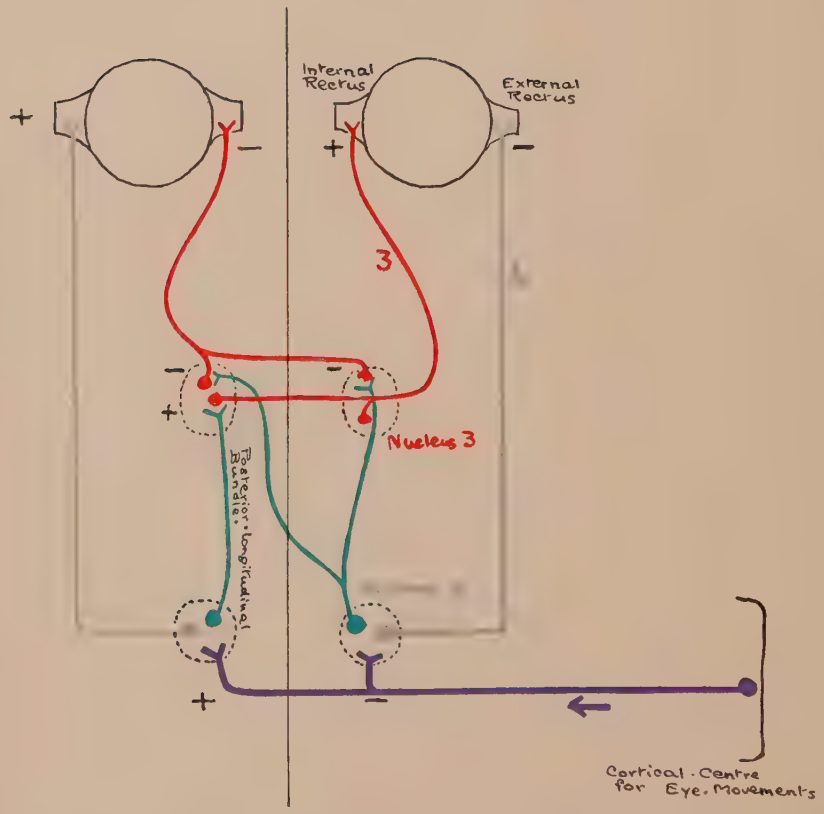

DIAGRAM 52.—Diagram to illustrate Sherrington's Experiment on the Reciprocal Innervation of Eye Muscles.

CHAPTER IX

LEVELS OF INTEGRATION AND MECHANISM OF CO-ORDINATED MUSCULAR MOVEMENT

ANY voluntary movement must involve the contraction of one group of muscles and the inhibition of the antagonists.

In considering any simple voluntary movement, muscles can be grouped into—

1. Agonists, or prime movers.
2. Antagonists, or muscles tending to interfere with the desired joint displacement.
3. Synergists, or muscles facilitating the precise movement.

In considering such a simple movement as clenching the fist, for instance, the *agonists* are the *flexors* of the fingers and thumb, the *antagonists* are the *extensors* of the fingers and thumb, while the *synergists* are represented by the *extensors* of the wrist.

It will thus be seen that some mechanism is necessary for the integration of nerve impulses to these different muscles, and this mechanism is supplied by the process of " reciprocal innervation " as described by Sherrington.

Reciprocal Innervation.

Muscles are innervated in such a way that the contraction of one or more muscles is accompanied by the simultaneous relaxation of the antagonistic ones, so that voluntary movement becomes possible.

Sherrington demonstrated this quality in an experiment on the eye muscles of the monkey. He cut the third and fourth nerves of the left eye, leaving the sixth nerve intact, so that the left external rectus was acting unopposed, and consequently rotated the eye outwards. Normally, if the left frontal lobe of the brain is exposed and stimulated, there is contraction of the right external rectus and of the left internal rectus. In Sherrington's experiment he exposed the left frontal lobe and stimulated it, but as the left third nerve had been cut, the left internal rectus muscle could not contract. The internal and external rectus muscles are antagonistic to each other, so that stimulation of one should lead to inhibition of the other ; consequently in this experiment, when the cortex is stimulated as described, the internal rectus cannot contract, but the external rectus can be inhibited. This actually occurs, so that the external rectus relaxes and the left eye moves back again to the mid-line.

(See Diagram 52.)

The same phenomenon can be shown in connection with the muscles of the thigh, and the reader is referred to the diagram for necessary details.

(See Diagram 53.)

Maintenance of Posture.

Posture, according to Sherrington, may be—

(*a*) Passive, or
(*b*) Active.

In the first case, it may be demonstrated by the position which a dead body takes up through the force of gravity, but active posture denotes a " reaction in which the configuration of the body and of its parts (in spite of forces tending to disturb them) is preserved by the activity of contractile tissues, these tissues then functioning statically."

Muscle tone has been described as the " raw material of posture," and efforts have recently been made to divide tone into—

1. Contractile tone.
2. Plastic tone.

This latter is responsible for the maintenance of position. Plastic tone is considered to hold the muscle at rest, and to maintain the intermediate postures through which muscles pass during the execution of movements, so that every advance made by contractile fibres is at once consolidated by the plastic elements. Hunter and Royle endeavoured to show that plastic tone is lost if sympathetic impulses to a muscle are cut off ; their work has not, however, been satisfactorily confirmed.

Maintenance of Tone.

This is governed by two reflex systems ; in the case of skeletal muscle, these are played upon by the cerebral cortex in the production of the voluntary action of the intact organism.

I. *The first reflex system*, which extends to a considerable degree up into the brain stem, maintains and regulates a steady tone, or " tonus," in the muscle, which is the basis of posture. This reflex tone arises in the muscles themselves, under the influence of that state of tension which obtains in them in varying degrees. This stimulus is known as the " stretch stimulus."

Variations in tone, and therefore in posture, are produced by continual reactions which arise in—

(*a*) The otolith organs.
(*b*) The proprioceptors throughout the body musculature.
(*c*) Receptors on the body surface, which subserve the sense of pressure.

Such reflexes are known as the " tonic standing and righting reflexes " of Magnus and De Kleijn, and may be secondary to phasic or movement reactions which are elicited from the exteroceptors. These reflexes of Magnus and De Kleijn have a very long latent period, and they continue unchanged so long as the stimulus which evokes them persists. This stimulus may be a variation in plane of the otolith membrane in the case of the labyrinths, or " stretch " in the case of proprioceptors.

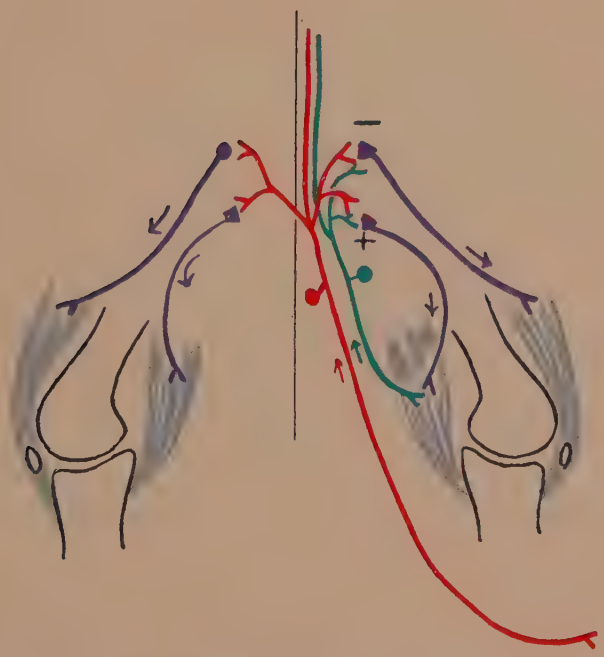

DIAGRAM 53.—Diagram to illustrate the Reciprocal Innervation of Antagonistic Muscles.

(*After Sherrington.*)

II. *The second reflex system* consists of short-lived movements, and its reflex arc does not extend above the spinal cord.

All these types of stimuli are analysed and compounded, so that the phasic and the tonic elements co-operate, balance is maintained, and a beautifully co-ordinated movement is produced. It must be observed that all reactions of both systems use one peripheral effector organ, which is the striated muscle, and one efferent pathway, *i.e.*, the motor neurone from the ventral horn of the cord, which is known as " the final common path."

Most of the work on the classification of these reflexes has been done on animals in which a state of *decerebrate rigidity* has been produced. This condition results when a trans-section of the brain stem is made between the level of the inferior corpora quadrigemina and the entry of the eighth cranial nerve. These studies have shown " that many different sense organs are involved, that very different centres integrate their stimuli, that the muscles concerned act in many different combinations in the production of the reactions, and that a whole series of diverse reflex groups are balanced together."

Postural Reactions.

The postural reactions of the body when at rest are known as " static reflexes " ; they include the reflexes of *pose*, in which the part of the body under consideration remains fixed in a definite position, and the *righting* reflexes by means of which pose is restored after disturbance. When the body is in movement, the postural reactions are known as stato-kinetic, and these reactions are produced by the initiation, cessation and variation of a movement.

MAGNUS' CLASSIFICATION.—I. STATIC REFLEXES.

A. Reflex Pose.

1. *Influence of the Head.*
   - (*a*) Tonic neck reflexes on limbs.
   - (*b*) Tonic labyrinth reflexes on body.
     - (i.) On limbs.
     - (ii.) On neck and trunk.
   - (*c*) Collaboration of neck and labyrinth reflexes.
   - (*d*) Indirect influence of labyrinth on limbs through action on neck reflexes.
2. *Indirect Influences on Posture.*

B. Compensatory Pose of Eyes.

(1) Tonic labyrinth reflexes on eyes.
(2) Tonic neck reflexes on eyes.
(3) Collaboration of tonic labyrinth and neck reflexes on eyes.
(4) Body postural reflexes on body itself.
(5) Visual postural reflexes.

II. Stato-kinetic Reflexes.

A. **Reactions to Rotation.**

1. Head reactions.
2. Eye reactions.
3. Reactions on body.

B. **Reactions to Progressive Movement.**

1. Reactions of head.
2. Reactions of extremities.

C. **Reactions to Partial Body Movements.**

This table serves to show how varied and widespread are these reactions, and a detailed account of these will be found in Lovatt Evans' " Recent Advances in Physiology " ; a few points may, however, be stressed.

The *head* is markedly the predominant feature determining body posture. *Righting reflexes* only come in when a trans-section is made cephalic to the thalamus, *i.e.*, when the whole of the mid-brain is left in continuity with the pons, medulla and cord. The centre for these reflexes is in the red nucleus. The grey matter of these long reflex arcs all lies within the brain stem, mid-brain, pons and medulla, while it should be noted that the efferent and afferent nerves never traverse the cerebellum. *Phasic reflexes* arise from the semicircular canals, and both phasic and tonic reflexes are present in an animal (from which the cerebral hemispheres have been removed but the thalamus left intact), even after removal of the cerebellum ; therefore neither the cerebellum nor the corpus striatum is essential to the *reflex* co-ordination of movement and posture. It would appear, however, that the cerebellum is essential to *voluntary* co-ordinated movement.

Cerebellum

There is a marked difference of opinion as to the exact functions of the cerebellum, and for this reason a separate chapter has not been devoted to the discussion of its functions. For our purpose, which is as far as possible to present these reactions as a whole, a short account of the main accepted views on cerebellar function is here inserted. It should be remembered that after a lesion of the cerebellum compensation by the opposite motor cerebral cortex follows very rapidly, so that investigation is extremely difficult.

As previously mentioned, the cerebellum is probably essential for the co-ordination of " voluntary " movement, especially that carried out by the extra-pyramidal system through the optic thalamus and the globus pallidus, but it is not concerned with postural reflexes. There is practically no localisation of function, its activity does not involve consciousness, and no alteration of sensation follows its extirpation. The cerebellum can " recoil " through the superior peduncle, red nucleus and optic thalamus on the cerebral cortex, and thus reinforce the action of the cerebral motor neurones. This upward tract relationship gives a structural basis for such disturbances as adiadokokinesis and delay in the beginning and ending of voluntary control. The cerebellum is also connected with the

lower motor neurones by the vestibulospinal path. Decerebrate rigidity is not abolished by removal of the cerebellum, but it disappears after section of the afferent nerve fibres from the muscles. The labyrinths are apparently not necessary for the production of the extreme tonus of this condition. The vermis is concerned with co-operation of movement involving bilateral muscles (Holmes).

Levels of Integration

Magnus and Sherrington differ as to where the integration of co-ordinated movement actually occurs, but it is essential to summarise briefly the possible levels which have both an anatomical and physiological basis for the part which they may play in this complex mechanism.

1. *Spinal cord—e.g.*, a simple spinal reflex.
2. *Upper part of the spinal cord*, where the nerves concerned with neck muscles derive their supply.
3. *Vestibular nuclei* (see connections of vestibular nerve, Part I., Chapter VI.).

   (The *afferent* stimuli at this level are those produced by the movement of fluid in the vestibular part of the internal ear, which may be due to the movement of the head. The efferent response may produce movements of the body by the vestibulospinal path, and of the eyes through the posterior longitudinal bundle.)
4. *Cerebellum*, the functions of which have been previously discussed.
5. *Between the entry of the eighth cranial nerve and the inferior corpora quadrigemina—e.g.*, Magnus' reflexes from the head and neck (see Table of Classification).
6. *Red nucleus* in connection with decerebrate rigidity.
7. *Thalamus* (see Part I., Chapter VII.).

TABLE TO COMPARE THE EFFECTS OF A LOWER MOTOR NEURONE LESION AND THOSE OF AN UPPER MOTOR NEURONE LESION

	Lower Motor Neurone (Anterior Horn Cells and Efferent Fibres).	Upper Motor Neurone (Betz Cells and Axons).
1. Wasting .	Prominent feature.	Slight, and only in consequence of disuse.
2. Reflexes .	Abolished in the affected segments, including "reflex tone."	Muscles are only flaccid during the period of shock. Tendon reflexes are always exaggerated. Plantar reflex usually gives an extensor response. Superficial abdominal reflexes often lost.
3. Rigidity .	Limbs tend to become flaccid.	Limbs tend to become rigid.
4. Paralysis .	Loss of all movements in the affected muscles.	No group is completely paralysed. Those devoted to skilled movements usually suffer first.
5. Electrical reactions.	Reaction to faradism and galvanism modified, or in complete lesions a typical "reaction of degeneration."	No obvious changes.
6. Contractures	Irregular deformities owing largely to the unopposed actions of non-paralysed muscles.	Rigidity accompanied by contractures in which the upper limb tends to become flexed and adducted, and the lower limb usually extended.

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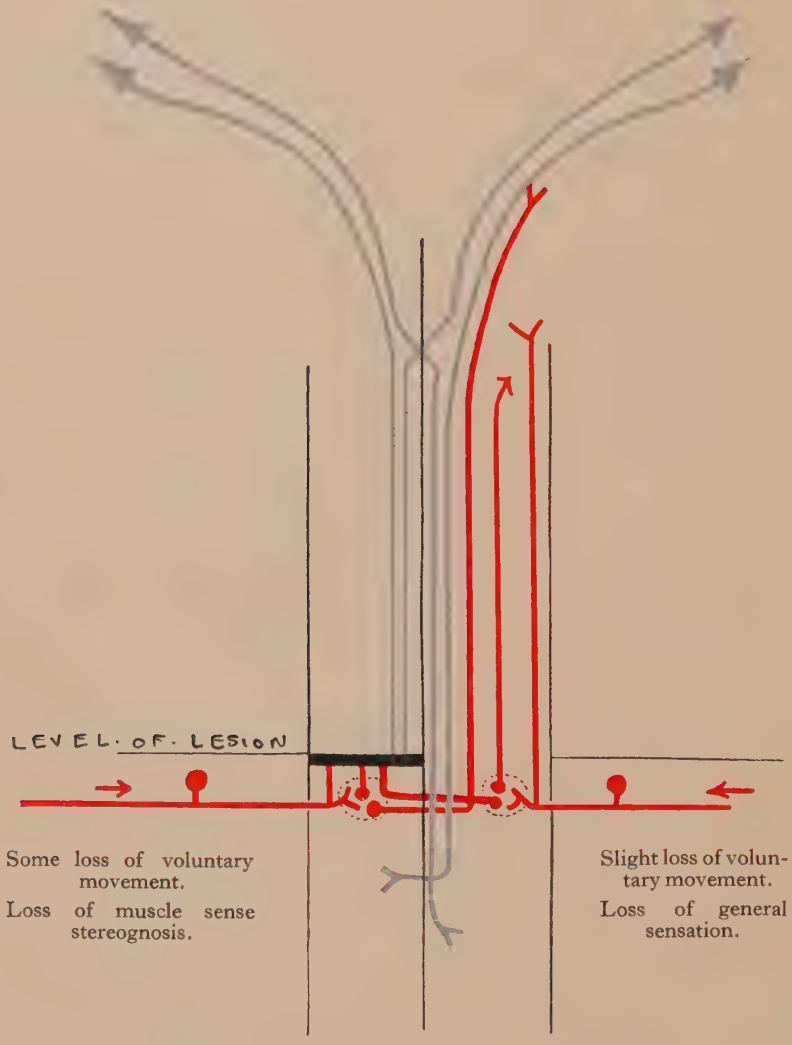

DIAGRAM 54.—Diagram illustrating Functional Effects of Hemisection of Cord.

CHAPTER X

NOTES ON CERTAIN PATHOLOGICAL CONDITIONS

In this chapter some account will be given of certain pathological conditions which are considered to be of importance in the study of the physiology of the nervous system. They are as follows :—

1. Hemisection of the Cord.
2. Complete Section of the Cord.
3. Aphasia.
4. Nystagmus.

1. Hemisection of the Cord.

Hemisection, or a unilateral transverse lesion, of the cord by trauma or disease results in morbid phenomena, to which the name of " Brown-Sequard's symptom complex " has been given. Obviously it is relatively rare to find a typical classical " Brown-Sequard condition," for disease usually does not cause a complete unilateral division ; more frequently the lesion is incomplete or else extends in addition partly over on to the opposite side of the cord. The classical description will be given, but the student must bear in mind that it will have to be modified in most cases. The reader is referred to Part I., Chapter II., for the effects of nerve section.

The sequelæ of a hemisection occur in those parts of the body distal to the site of the lesion, and they may be divided into—

(*a*) Changes on the same side as the lesion.
(*b*) Changes on the opposite side.

(See Diagram 54.)

(*a*) On the Same Side.

(1) *Motor paralysis* of the same side below the level of the lesion. This paralysis is " spastic " in nature, because there is interference with the cortico-spinal path.

(2) *Vasomotor paralysis* of the same side occurs, the skin in the early stages being reddened and warm, but later a chronic condition of cold and cyanosis supervenes. This is due to interruption of the vasoconstrictor fibres of the lateral column of the same side.

(3) *Disturbance of deep sensibility* occurs distal to and on the same side as the lesion ; consequently, even when motility is restored to these parts, ataxia (incoordinated gait) is a prominent feature, and is due to interference with the posterior columns and the spinocerebellar tracts.

(4) *Superficial hyperæsthesia* is found, and is not readily explained, but may be due to the fact that, as tactile impressions are partly crossed and partly uncrossed

at any given level, only the crossed fibres can convey impressions upwards from the same side as the lesion. This means that extra work is thrown on these fibres, and the cells of the dorsal horn pass on " summated " stimuli, so that until adaptation of the organism to the new condition has occurred painful impressions are received. It should be noted that this phenomenon is transitory.

(5) *Flaccid paralysis* occurs in groups of muscles corresponding with the half-segment affected, due to a lower motor neurone type of paralysis.

(6) *Complete anæsthesia* of all forms for the affected half-segment, due to a lesion of the lowest sensory neurone.

There is usually a zone of cutaneous hyperæsthesia in the skin area corresponding to the peripheral distribution of the posterior nerve root entering the cord just above the level of the lesion.

(*b*) On the Opposite Side.

Superficial anæsthesia occurs on the side opposite to the lesion, so that there is loss of pain, heat and cold, due to interference with the spinothalamic and spinotectal tracts after the decussation of their constituents.[1]

The reader is reminded that if the lesion is below the upper thoracic region all the fibres of the direct pyramidal tract will have crossed, so that those injured will be supplying the same side of the body as the lesion. Also, with a lesion in the thoracic region the intercostal muscles of the same side are paralysed, and with an upper cervical lesion the same side of the diaphragm is paralysed.

There are in addition certain *reflex changes* which may be summarised.

(1) At first there is loss of muscle tone at the level of the lesion, due to destruction of the spinal arc. After the stage of shock is over tone returns to the muscles below the level of the lesion, and consequently reflex response reappears.

(2) When the lesion is above the lumbar region, defæcation, micturition and parturition still occur as usual, as central control is bilaterally represented.

(3) The vascular dilatation and dryness of the skin on the side of the lesion are more marked when the hemisection is in the thoracic region, because of interference with the path from the medulla to the accessory vasomotor centres in the cord.

(4) The knee jerk is increased on the side of the lesion, due to the cutting off of controlling impulses from the higher centres.

(5) The plantar reflex becomes " extensor " on the side of the lesion, due again to the general law of " release of function in the nervous system," by which when a higher centre is cut off lower centres are released and exhibit their independent and more primitive activities.

2. Complete Section of the Cord.

This condition may occur as a result of trauma or of disease, and investigation has been very completely undertaken by Head and by Riddoch in connection with war injuries.[2]

In civil life section of the cord is usually slowly progressive, and then the initial stage of shock does not occur. In cases of acute trans-section there is

always an initial stage of shock which varies in its duration, sometimes lasting up to sixteen days or more, and exists only in the part of the body distal to the lesion. The intensity varies with the position of the organism in the animal scale, and is therefore most extreme in man. After a varying period, if the patient survives, reflex action begins to return. The level of the lesion is responsible for a varied series of signs, and these may be briefly summarised :—

(*a*) In the *upper cervical* region a simultaneous paralysis and anæsthesia affect the four extremities and the trunk.

(*b*) In the *dorsal* region the lower extremities and the lower half of the trunk are affected.

(*c*) In the *lumbar* region only the lower limbs are involved, producing a paraplegia.

At whatever level, however, the lesion occurs, there is complete abolition of sensation and of movement below that level.

The loss of *sensory* function is complete, as all the ascending tracts are interrupted, while there is an absolute paralysis due to interference with the pyramidal tracts and also of every link between the cortex and the spinal motor centres.

Motor Changes.

(1) In complete division of the cord in its upper region, during the early stages there is complete muscular atony and abolition of reflexes in the paralysed regions. This is expressed in " Bastian's law," and there are many theories to account for its occurrence, none of which appear to be adequate.

(2) Muscles of the bladder and rectum are involved, so that retention of fæces and urine occurs. When, however, the distension of the bladder reaches a certain point, overflow incontinence ensues. If, as rarely happens, the patient survives, reflex micturition and defæcation become re-established.

(3) There is vascular dilatation, due to vasomotor paralysis in the paralysed region, followed later by cold and cyanosis due to chronic vascular relaxation. Similarly, the marked engorgement of the corpora cavernosa is due to vasomotor disturbance.

(4) General flexion spasms, as part of the " mass reflex."

(5) Erection, micturition and profuse sweating (known as mass reflexes) may be elicited by pinching the skin anywhere below the lesion, except in a narrow band corresponding to the lesion itself when the spinal arc is interrupted. The sweat fibres to the head and neck arise from the first and second thoracic segments, so that with a lesion at the level of the first thoracic segment the whole body would sweat when the mass reflex was elicited.

Sensory Changes.

(1) Complete loss of all sensation below the level of the lesion.

(2) Temporary hyperæsthesia in an area above the anæsthetic zone and sometimes a corresponding area of muscular tonic spasm from heightened reflex irritability.

3. **Aphasia.**

By this term is meant " the loss of intelligent speech," the word " speech " being taken to include the appreciation and the production of both the written and the spoken word. True aphasia should be distinguished from the condition known as dysarthria: the latter is due to a pure motor breakdown, either local or central, which causes a difficulty in the actual motor performance, and which may occur in the course of many diseases.

Speech is the most highly evolved and the most complicated function of the brain, and any analysis of the mechanism involved must of necessity be somewhat crude. The many varying views on the subject will be found set forth in Head's monograph on aphasia, but a working hypothesis can be deduced from a survey of certain fundamental facts.

It is essential to regard the mechanism of speech as a whole. There seems to be no doubt that certain regions of the brain are definitely connected with definite elements of the speech mechanism, although interference with any part of the mechanism may be due to a lesion on the connecting paths rather than to a definitely localised cortical condition. There are five areas of the brain that appear to be more particularly concerned with speech (see Diagram 55):—

A. *Post-Rolandic Area*, concerned with appreciation of general sensation.

B. *Spoken Speech.*

(i.) Sensory aspect: auditory-psychic area, concerned with the interpretation of afferent impulses reaching the adjacent auditory sensory area.

(ii.) Motor aspect: glossokinæsthetic area, concerned with the production of spoken speech through the adjacent labio-glossomotor area.

C. *Written Speech.*

(i.) Sensory aspect: visuopsychic area, concerned with the interpretation of afferent impulses reaching the adjacent visuosensory area.

(ii.) Motor aspect: cheirokinæsthetic area, concerned with the production of written speech through the adjacent cheiromotor area.

Although these regions are especially concerned, it is probable that the simplest act of " speech " involves the activity of all parts of the cerebral cortex, and if one element of the mechanism is interfered with the whole function of speech becomes abnormal. Interference may occur with a cortical area, but more frequently a lesion involves the association paths between the areas or the afferent or efferent paths connecting with the areas, and consequently the resulting functional disturbance becomes complex.

To take a simple example, a lesion involving the cheirokinæsthetic area only, or isolating this area, leads to inability to write what is desired. The individual can write because the motor area is not involved, but he is unable to call up memories of previous similar movements and so cannot write what he wishes to. Similarly, a lesion of only the glossokinæsthetic area renders an individual unable

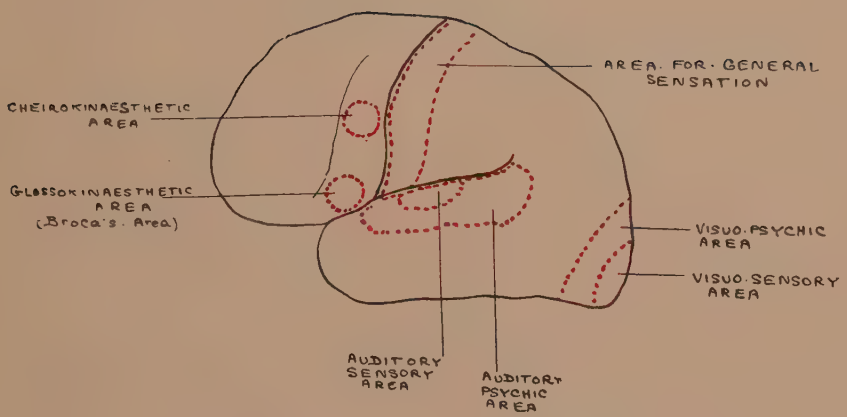

DIAGRAM 55.—Diagram to illustrate Position of Centres chiefly concerned in Mechanism of Speech.

to say what he wants to, although he can speak; but he hears himself say the wrong thing and knows that it is wrong. This illustrates the way in which motor speech is kept at a high level of accuracy by correction through sensory paths. Again, a lesion isolating the visuopsychic area leads to inability to understand what is seen : a man cannot read, although he can see, because he cannot compare his visual impressions with memories in the visuopsychic area, and so he does not interpret what he sees. Similarly, a lesion involving the auditory-psychic region produces inability to understand spoken speech, although the man can hear.

The intimate connection between the various parts of the cortex in respect of this function of speech is shown in the case of a man who becomes blind, *i.e.*, his visuosensory area is no longer being stimulated. The visuopsychic area, with its stored memories, can still, however, be aroused to activity by sensory paths other than the usual visual one ; for example, the feel or the sound of a cat will still call up an image of the appearance of the animal and of other visual memories therewith connected.

Speech functions which are more recently acquired tend to drop out before those learnt in early life ; similarly, a man who is a good linguist loses the power of speaking the last-learnt foreign language rather than one he acquired early in his career. A child learns speech in its elements, whether spoken or written, but when once this faculty is developed we receive speech in a " running pattern " of which the individual elements are disregarded. The breakdown of some association path may then lead to inability to produce a particular word of command, although that word can be used in the run of a pattern. This is exemplified by the patient who, after many attempts to produce the word " No," said : " I am very sorry, sir, but I can't say ' No,' sir."

Head divides aphasia into four types [3, 4] :—

(*a*) *Verbal.*—There is defective word formation, either written or spoken, or both ; this is usually associated with a lesion in the posterior end of the inferior frontal convolution.

(*b*) *Nominal.*—There is defective naming of letters, words, or objects ; this is found associated with a lesion of the angular gyrus.

(*c*) *Syntactical or Jargon.*—Speech is voluble and rapid, but entirely senseless, because there is loss of correction by other sensory paths ; this occurs with lesions of the superior and middle temporal convolutions.

(*d*) *Semantic.*—There is inability to retain a complete conception in the mind ; this is associated with a lesion of the supramarginal gyrus.

The following terms are used in connection with the subject of aphasia : —

Alexia. Word-blindness, inability to appreciate the written word.

Anarthria. Impairment of the motor powers of expression (Head's verbal aphasia).

Apraxia. Inability to do as desired.

Agnosia. Inability to appreciate meaning.

Agraphia. Inability to write.

4. **Nystagmus.**

Normally the eye is kept at rest in the central position by the postural mechanism ; this produces a steady gaze.

In abnormal conditions, however, deviation of 10° to 30° away from the central point occurs, so that on looking fixedly at an object elsewhere in the visual field jerking movements are produced, which condition is known as nystagmus. This condition occurs whenever there is any lesion affecting the maintenance of postural mechanism of eye movements, and is the endeavour of the eyes to compensate for the lesion.

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APPENDIX

HISTOLOGICAL METHODS

THE following simple methods of investigating nervous structures give reliable results. Further details can be found under the given references.

A. NERVE CELLS.

1. *Film Preparation.*

Spread a thin film evenly ; dry in air.
Fix in 80 per cent. alcohol for fifteen minutes.
Stain in Löffler's methylene blue for ten to twenty minutes.
Wash in methylated spirit.
Differentiate if necessary in 75 per cent. alcohol, or in acid alcohol (HCl, 1 c.c. ; alcohol, 70 c.c. ; water, 30 c.c.).
Dehydrate in absolute alcohol.
Mount in Gurr's neutral mounting medium.
(N.B.—Nissl granules dark blue, nuclei paler blue.)

(Hall and Herxheimer, p. 221.)

2. *In Tissues.*

(*a*) Picrocarmine method.

Fix in 10 per cent. formol for forty-eight hours.
Transfer to Müller's solution for any period up to six months.

(Potassium bichromate	2·5 gm.
Sodium sulphate	1 gm.
Water	100 c.c.)

Embed and section in usual way.
Stain from water with Stöhr's (or Ranvier's) picrocarmine for at least twenty-four hours.
Wash in methylated spirit (not water).
Dehydrate and mount in usual way.

(Stirling, p. 66.)

(*b*) Aniline blue-black method.

Fix in 10 per cent. formol for twenty-four hours.
Wash, embed, and section in usual way.
Stain from water with a good blue-black ink, controlling degree of stain under low power.
Wash, dehydrate, and mount as usual.

B. MYELINATED NERVE FIBRES.

1. *Osmic Acid Method* (Robertson-Heller).

Fix in 10 per cent. formol for eight to ten days.
Wash, embed, and section in usual way.
Stain from water in 1 per cent. osmic acid for at least thirty minutes in the dark.
Transfer to 5 per cent. pyrogallic acid, thirty minutes.
Differentiate in 0·25 per cent. $K_2Mn_2O_8$, thirty + minutes.
Wash, dehydrate, and mount as usual.

(Hall and Herxheimer, p. 183.)

2. *Hæmatoxylin Method* (Weigert-Pal).

Fix thin pieces in 10 per cent. formalin for one week.
Transfer to Müller's fluid for one week.
Mordant for one week in—

Potassium bichromate	5 gm.
Fluorchrome	2·5 gm.
Water	100 c.c.

boiled and filtered.

Take through spirits, dehydrate, clear and embed as usual.
Sections at least 30 μ thick.
Mordant from water for thirty minutes in—

Neutral copper acetate	5 gm.
Fluorchrome	2·5 gm.
Water	100 c.c.

boiled and 5 c.c. acetic acid 36 per cent. added.

Transfer to Kulschitsky's hæmatoxylin for twenty-four hours in incubator at 37° C.

(Hæmatoxylin . . . 1 gm. dissolved in a little absolute alcohol.
Acetic acid, 2 per cent. . 100 c.c.)

Wash in tap water.
Differentiate in 0·25 per cent. $K_2Mn_2O_8$, thirty seconds.
Wash in water.
Transfer to Pal's solution

(Oxalic acid	0·5 gm.
Potassium sulphite	0·5 gm.
Water	100 c.c.)

for some seconds; wash in water.
If necessary, repeat treatment with $K_2Mn_2O_8$ and Pal's solution until "grey" substance is colourless and "white" substance is dark blue. Wash. Dehydrate and mount as usual.

(Hall and Herxheimer, pp. 178–180.)

C. Axis Cylinders of all Nerve Fibres.

Some one of the modifications of the Bielschowsky silver methods should be used. The technique must be followed exactly. Details will be found in Lee, pp. 573–582. Da Fano's modifications are the best.

D. Neuroglia (method of Lhermitte and Guccione).

Fix in 5 per cent. formol fifteen days.
Wash in running water for several hours.
Cut frozen sections; transfer to distilled water.
Transfer to saturated aqueous mercuric chloride, two hours.
Mordant for forty-eight hours in—

1 per cent. chromic acid	50 c.c.
1 per cent. osmic acid	12 c.c.
2 per cent. acetic acid	8 c.c.
Distilled water	30 c.c.

Wash in distilled water; transfer to a slide.
Flood the slide with—

Victoria blue (Grübler)	1·5 gm.
Distilled water	100 c.c.

(Warm to dissolve, and filter.)

Warm above a flame until it steams ; cool ; repeat at least twice.
Pour off stain and cover with Lugol's solution

(Iodine	1 gm.
Potassium iodide	2 gm.
Distilled water	100 c.c.)

for one minute.
Blot carefully.
Differentiate in aniline-xylol (equal parts), controlling under low power until neuroglia is dark blue.
Remove all trace of aniline with xylol.
Mount in Canada balsam.

(Carleton, p. 264.)

E. Nerve Endings.

1. *Gold Chloride Method.* (Loewit.)

Place small piece of fresh tissue in 30 per cent. formic acid, one minute.
Transfer to 1 per cent. $AuCl_3$ twenty minutes in dark.
Place in 25 per cent. formic acid in dark, twenty-four hours.
Transfer to glycerine for examination.
If not sufficiently reduced, add formic acid to the glycerine.
(Nerve endings dark purple.)

(Stirling, p. 78.)

2. *Vital Methylene Blue Method.*

Remove tissue with as little injury as possible and spread on slide.
Treat with 0·05 per cent. methylene blue in isotonic saline (0·6 per cent. NaCl for frog, 0·85 per cent. NaCl for mammal) for twenty minutes, covered with watch-glass lined with moist filter paper.
Drain off stain ; examine in isotonic saline.
(Nerve endings dark blue, not permanent.)
The dye can be used also by injection.

(Langley, pp. 125 and 321.)

3. *Sihler's Hæmatoxylin Method.*

Place small portion of tissue for one day in—

Acetic acid fort.	10 c.c.
Glycerine	10 c.c.
1 per cent. chloral hydrate	60 c.c.

Transfer to glycerine for two hours.
Stain for three to ten days in—

Ripe hæmatoxylin solution	10 c.c.
Glycerine	10 c.c.
1 per cent. chloral hydrate	60 c.c.

Differentiate in acetic acid-glycerine (equal parts).
Preserve in glycerine.
(Nerve endings dark purple.)

(Langley, p. 131.)

F. Degenerating Nerve Fibres (Marchi's method).

Fix in 10 per cent. formalin at least one week.
Transfer thin pieces to Müller's fluid for fourteen days.
Place straight in Marchi's fluid.

(Müller's fluid	2 parts.
1 per cent. osmic acid	1 part.)

Leave for one month, keeping solution fresh.
Transfer to 50 per cent. alcohol, then to 75 per cent.
Keep changing the 75 per cent. alcohol until it remains clear.
Dehydrate quickly, embed, and cut about 50 μ thick.
Mount in usual way.
(Prolonged treatment with strong alcohol or xylol should be avoided.)
Degenerating nerve fibres are black.

(Hall and Herxheimer, p. 207.)

NOTES

1. When dealing with blocks of tissue that will give large sections, it is better to embed in celloidin rather than in wax, as the celloidin prevents the tissues from breaking in subsequent manipulations, and also allows of the cutting of thick sections.

2. *Weigert-Pal Method for Myelin.*—The principle of this method is that all the structures are intensely stained with hæmatoxylin after double mordanting. The $K_2Mn_2O_8$ oxidises the hæmatoxylin to a colourless substance, and itself gives rise to MnO_2; the MnO_2 is then converted into $MnSo_4$, which is colourless and soluble, and this is then washed away. This process will naturally take place most readily in the open grey matter, and should be interrupted when this appears light; the dense myelin keeps the stain more tenaciously.

3. *Marchi's Method for Degenerating Myelin.*—Osmic acid blackens normal myelin because of the presence of oleic acid, which reduces it to the black OsO_2. Preliminary treatment with the potassium bichromate in Müller's fluid oxidises the oleic acid, and the myelin does not blacken on subsequent treatment with osmic acid. Degenerating myelin contains large quantities of very unsaturated fatty acids greatly in excess of what is oxidised by short treatment with potassium bichromate; in this case, therefore, the degenerating fibres still blacken on treatment with osmic acid. The reaction can be obtained about forty hours after the lesion, increases in intensity up to fourteen days, and after about forty-four days is usually absent owing to the removal of the broken-down material.

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